BENTE, PETER JAMES
NESTING BEHAVIOR AND HUNTING ACTIVITY OF THE GYRFALCON, FALCO RUSTICOLUS, IN SOUTH CENTRAL ALASKA.

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NESTING BEHAVIOR AND HUNTING ACTIVITY OF THE GYRFALCON, *Falco rusticolus*, IN SOUTH CENTRAL ALASKA

A

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Peter J. Bente, B.S.

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NESTING BEHAVIOR AND HUNTING ACTIVITY

OF THE GYRFALCON, Falco rusticolus,

IN SOUTHCENTRAL ALASKA

RECOMMENDED:

Chairman, Advisory Committee

Program Head

Director, Division of Life Sciences

APPROVED:

Vice Chancellor for Research and Advanced Study

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ABSTRACT

Nesting behavior and predation in two pairs of Gyrfalcons (Falco rusticolus) were studied intensively during April through September in 1975 and 1976 in the Alaska Range, Alaska. Early season behavior involving mutual displays gave way to separated roles of the sexes. Throughout the nesting season, males provided prey for females and nestlings. Females remained sedentary, conducting incubation (94 %), brooding (99 %), nestling feedings (89 %), food caching (93 %) and retrieval of cached prey (96 %). Occasional hunting forays by the female began when the nestlings were 17 days old. Mean length of hunting forays was 91.2 and 21.7 minutes for the male and female, respectively.

Prey species varied seasonally; arctic ground squirrels (Spermophilus parryii) were taken frequently during summer. Gyrfalcons responded opportunistically to experimental releases of supplemental prey. This opportunistic strategy has probably helped to maximize breeding success under the conditions of varying prey abundance typical of northern environments.

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INTRODUCTION

Biological study of the Gyrfalcon (Falco rusticolus) is timely because human access to their circumpolar habitat is increasing as exploraton for minerals, petroleum and other resources is increasing in northern regions. Interest in Gyrfalcons is high because they nest regularly in tundra and alpine-tundra regions, are the largest of the falcons (Falconidae), and have a long cultural history of use by man for falconry (Cade 1968). Despite this interest, the behavioral biology of the species has been intensively studied by only a few researchers in widely separated areas of the world (e. g., Cade 1960, Dementiev 1960, Roseneau 1972, Platt 1977 and Jenkins 1978).

Previous works by Dementiev (1951, 1960), Hagen (1952), Cade (1960), White and Weeden (1966), White and Cade (1971), Roseneau (1972), Jenkins (1974, 1978), Platt (1976, 1977) and Langvatn (1977) have contributed to our knowledge of distribution, food habits and basic ecology, but detailed information on breeding behavior is still lacking. Platt (1977) discussed breeding behavior in relation to the environment and human disturbance in northwestern Canada, and Jenkins (1974, 1978) observed the behavior of pairs with nestlings in Greenland. This study of nesting and predatory behavior of pairs breeding in south central Alaska adds to these works.

In this study, supplemental prey were released near active eyries to help identify the predatory behavior of Gyrfalcons. The response to these conditions of locally abundant prey (created by the experiments) was used to evaluate the type of predation practiced by Gyrfalcons. Slobodkin (1962, 1964) described two methods of predation, prudent and imprudent. This and other information has been employed to identify the strategy of predation used by Gyrfalcons nesting in a subarctic region.

By increasing our understanding of Gyrfalcons it may be possible to use them as indicators of environmental quality, utilizing the concepts outlined by Olendorff and Kochert (1975) and Olenfdorff and Stoddart (1974). This may be particularly useful and important since resource development in northern regions will continue to occur in areas where Gyrfalcons nest.

OBJECTIVES

Gyrfalcons were studied during the summer breeding season to determine their nesting behavior, hunting activity, seasonal use of prey, and response to the experimental release of supplemental prey in the nesting area.

Until recently, the nesting behavior of large falcons has been mostly undescribed. Behavioral studies of Peregrine Falcons (Falco peregrinus) (Nelson 1970, 1977), Prairie Falcons (Falco mexicanus) (Enderson, 1964), and Gyrfalcons (Jenkins 1974, 1978, Muir 1974, Platt 1977) have been stimulated by the need for accurate behavioral descriptions at a time when many raptors are subjected to global environmental contamination (Newton 1976, 1979). Pollutants that pose serious threats to raptors are chlorinated hydrocarbon pesticides and polychlorinated biphenyls, and it is possible that individuals of affected species may exhibit behavioral and physiological anomalies (Peakall 1976, Ratcliffe 1980). Behavioral changes may be partially responsible for the poor rates of reproduction observed in recent years (Nelson 1976). Gyrfalcons are not seriously threatened because they reside in areas where development is not occurring rapidly. Walker (1973,1977) has shown that levels of pollutant residues were generally low in Gyrfalcon populations from the Seward Peninsula, Alaska, although some individuals carried moderate amounts

of pollutant residues. The purpose of recording the nesting behavior of Gyrfalcons is to expand our knowledge of this species and to provide information on behavioral variations expressed by individual Gyrfalcons. These data may prove useful in comparison to the behavior of other large falcons (which may or may not be affected by pollutants).

Newton (1979) has described sex-based differences in the hunting activity of raptors. Hunting by this species was observed to establish the role performed by each sex. These data were integrated with studies of food habits to determine hunting ranges and prey use during the breeding season. Food habits analyses were also conducted to document seasonal variations in prey captured by Gyrfalcons.

Releases of supplemental prey near active nest sites were performed to determine the response of Gyrfalcons to locally abundant prey resources. These experiments also helped determine changes in the frequency and timing of hunting by adults, the use of caching areas, and the length of time required to capture all of the prey at the release stations. Information gained from these studies was used to evaluate the predatory strategy of Gyrfalcons.

STUDY AREA

Field studies of Gyrfalcons were conducted in the Alaska Range in south central Alaska (Figure 1). This area is similar to Mount McKinley National Park. Descriptions of climate, habitats, vegetation, and fauna for the Mount McKinley area (Dixon 1938, Murie 1946, 1963) also apply to the study area.

The general geology (summarized by Beikman 1974) and geomorphic history of the study area influences the availability of nesting habitat for cliff-nesting raptors. Cliffs used by raptors are found at elevations approximately 1475 m above mean sea level (asl). Broad, glaciated valleys (1030 m asl) separate potential nesting cliffs and provide habitat for prey species. Other glacial topographic features (moraines, eskers, kettles) provide excellent habitat for the major prey species used by Gyrfalcons.

The vegetation in this region is mostly 'shrub tundra' and 'mat cushion tundra,' although spruce forests (Picea glauca) are found in lowland areas and rock barrens occur extensively at high elevations (Viereck and Dyrness 1980). Several avian habitat types, as defined by Kessel (1979), occur in the area: lacustrine and fluvatile waters, cliffs and block fields, dwarf shrub meadow and low to medium shrub thickets.

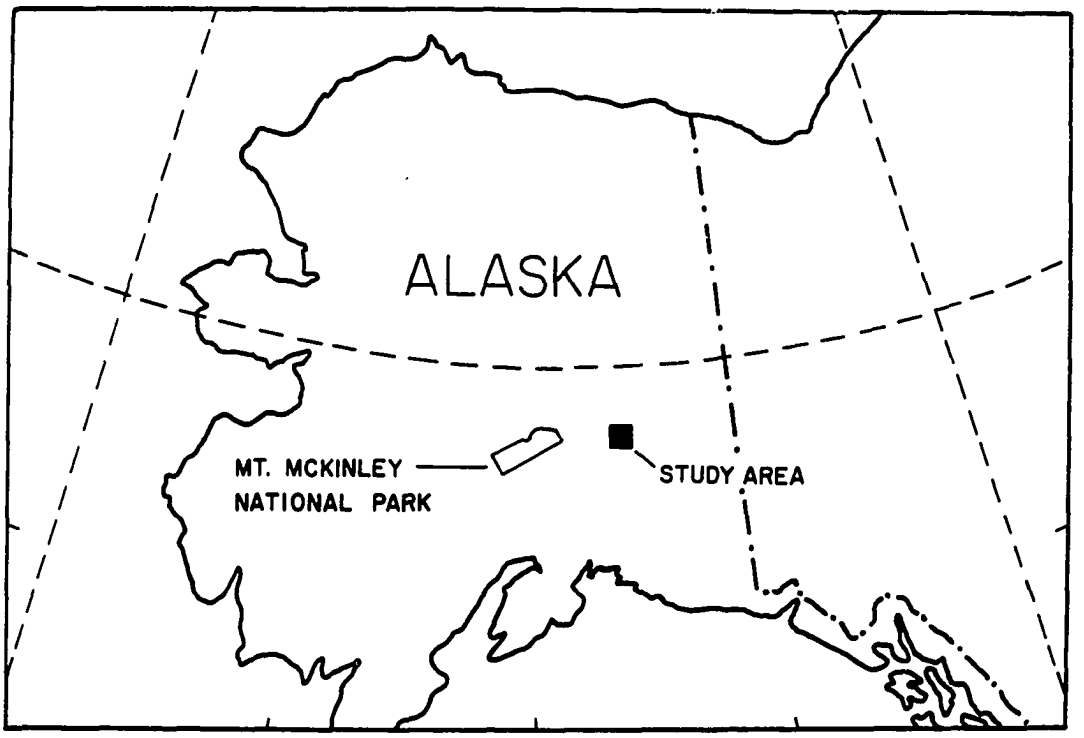

Figure 1. Location of study area in south central Alaska.

METHODS

Gyrfalcon nesting habitat was surveyed in the Alaska Range on skis, snowshoes and snowmachine during March through May in 1975 and 1976. On 21 May 1975, a nest with two recently-hatched young was found. In 1976, the intensive study site was selected during the early incubation period (3 May).

Nesting activities and behavior were observed at one location in each year. A blind was constructed approximately 50 m from a nest in 1975 and 60 m from a nest in 1976. In each year people approaching and entering the blind were clearly visible to the nesting Gyrfalcons. As a result, the adult falcons were mildly disturbed during the first week of observations. Once an observer was inside the blind the adult falcons soon resumed normal behavior, although the male did not adjust as quickly as the female. After the first week, the falcons often watched as observers approached the blind, but they were not visibly disturbed by the presence of observers.

Observations from the blind were made on 74 different days (8 days in 1975 and 66 days in 1976) for a total of 538.4 hours of observation. During 1975, observations were limited to 64.6 hours of the nestling stage. In 1976, 473.8 hours of observations were obtained during 14 days of the incubation period, 45 days of the nestling stage and 7 days of the fledgling period (Figure 2).

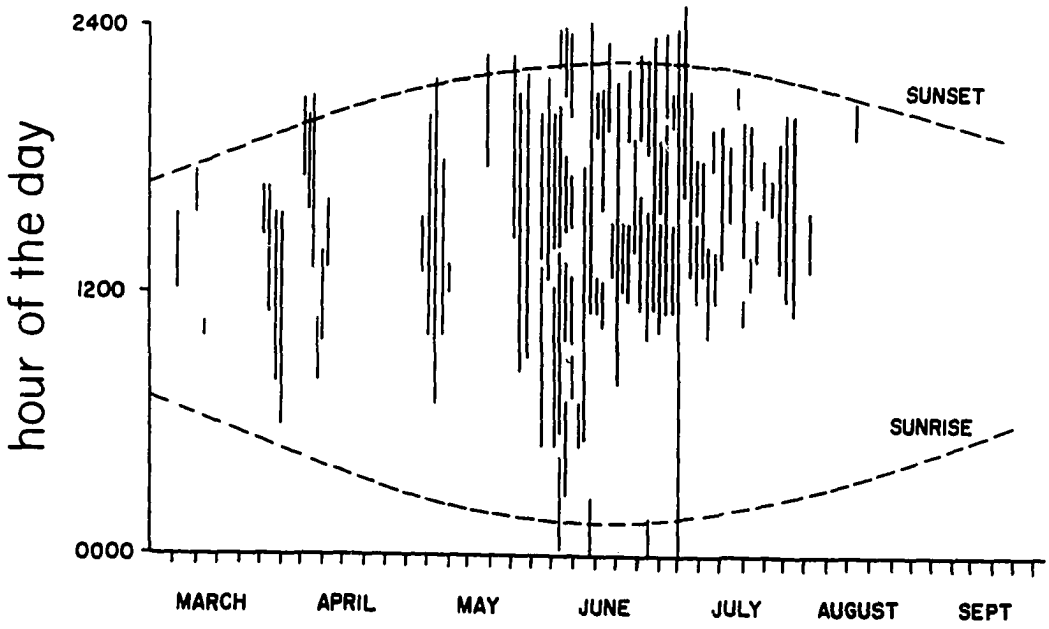

Figure 2. Times of daily observations of nesting activities, 1976.

The food habits of Gyrfalcons were determined by collecting prey remains and pellets following the methods outlined by Errington (1932) and Roseneau (1972). Collections were made at least biweekly during April through September at three nesting locations. These data represent a total of four nestings by Gyrfalcons in the two year study period (one nest was active only in 1975, one nest was active only in 1976, and one nest was active in both years). Because of small sample sizes, only qualitative statements concerning the diet of Gyrfalcons have been included. Roseneau (1972) demonstrated the need for large sample sizes to come to quantitative conclusions about the prey selected by Gyrfalcons.

In both years, radio telemetry was used to find the locations of free ranging adult Gyrfalcons (Dunstan 1972). One adult male was followed for five days in 1975, and an adult female was followed for 10 days during the mid-nestling period in 1976. The transmitters were attached to the central rectrices of the adult birds with dental floss and acrylic cement. The radio packages were dislodged from the rectrices in less than two weeks. No attempt was made to re-mark either bird because of the advanced stage of molt exhibited by each bird during the initial capture. Each radio was recovered; one was below a perch and one was on the tundra. It was confirmed that the transmitters were either bitten or pulled off of the feathers. There was no

evidence to suggest that premature molt was caused by the additional weight (15 - 20 g) of the radio.

To evaluate the predation strategy of Gyrfalcons supplemental prey were released near the nest sites studied in 1975 and 1976. Domestic chickens (Gallus gallus var. Cornish Cross or White Leghorn) and Japanese Quail (Coturnix coturnix) were color marked with leg bands and released on the tundra as prey for the Gyrfalcons. Japanese Quail could not survive long enough and were not taken as prey by the falcons; consequently they were not used in 1976. Chickens (approximately 3 - 5 weeks old) were first tethered in obvious locations to allow the Gyrfalcons to become aware of the unaccustomed prey. Tethers were light weight thread or twine that could be broken by the falcons during prey capture. Once predation of chickens began the chickens were permitted to range freely on the tundra. Free-ranging chickens did not wander more than 50 m from the water and food provided for them.

Supplemental prey were released within 0.5 km of the Gyrfalcon nest site. These locations were not visible from the nest site but were visible from perches often used on the nest-cliff. Chickens were usually released in small groups (4 - 6), although occasionally individuals were placed on the tundra.

Throughout the text the definitions of Ratcliffe (1962) are used when referring to nest-cliffs, nest sites and

eyries. Names for the developmental stages of young falcons follow the classification of Skutch (1961). The American Ornithologists' Union checklist (A.O.U. 1957) and the 32nd and 33rd supplements were used for the nomenclature of bird species. All times noted in the text are Alaska Daylight Time (ADT).

RESULTS AND DISCUSSION

Migration and Winter Distribution

The Gyrfalcon is considered a semi-migratory species. Some portions of the population are non-migratory, whereas other portions are moderately migratory. Some evidence supports Platt's hypothesis that immature and subadult birds are the most mobile (Platt 1976) and that adults are generally resident on the nesting grounds; however, T. L. Fleming (personal communication, 1980) has regularly observed some adults in the State of Washington (55 N). This indicates that some adults travel long distances to the south during the fall and winter. Since resident Gyrfalcons are obligate ptarmigan (Lagopus spp.) predators during the winter (Cade 1960, Gudmundsson 1970), incursions of adults into southern regions may reflect low winter ptarmigan populations in northern regions (Dementiev 1960). Gyrfalcons are capable of residing in the arctic if prey are available. Their semi-migratory nature is probably influenced by shifts in prey abundance and extreme environmental conditions.

Platt (1975, 1977) observed that adults often remain in the arctic during the winter months and he suggested that the sexes remain apart. They were not found together on the breeding territory until courtship begins in early March. This separation of adults during the winter was based on

relatively few observations and it may not be typical of the species. There was some evidence to show that adults remain together as pairs through the winter during this study. Both Platt and I have few winter observations and more detailed information will be needed to elucidate winter distribution patterns of Gyrfalcons.

In the Alaska Range there are several locations where adults have been observed throughout the winter. Since this area was near the southern breeding limit of the species, the presence of over-wintering adults is not unusual. Dementiev (1960) also observed that Gyrfalcons were resident in the southern portions of their range in Asia. The observations of Sheldon (1909), Murie (1946, 1963), Gabrielson and Lincoln (1959) and Cade (1960) provide other evidence that Gyrfalcons may be seen regularly in the Alaska Range during the winter.

Three pairs remained near their nest-cliffs during the winter in the present study area. Two of these winter observations followed successful breeding by the pairs during the previous nesting season. In 1971 - 1972, a pair was observed frequently throughout the winter by John C. Schandelmeier (personal communication, 1975). The pair remained in a broad valley and fed upon ptarmigan and a small flock of Mallards, Anas platyrhynchos, that remained at an open groundwater spring. The Gyrfalcons killed all of the ducks and often followed Schandelmeier to take

ptarmigan that he flushed while he was checking his winter trapline. In the early 1970's, Schandelmeier also repeatedly observed a pair during the winter near another area where Gyrfalcons have been known to nest. A third overwintering of a Gyrfalcon pair in close proximity to their nesting cliff was observed by David Lani (personal communication, 1976). These birds were seen in the vicinity of a traditional eyrie that has a long history of use for nesting (Cade 1960). Although unconfirmed, it is probable that the pair seen by Lani nested at this cliff previous to the winter observations.

In other areas Gyrfalcon pairs have remained in or near their nesting territories during the winter. David G. Roseneau learned that one pair remained near its nest site throughout the winter on the Seward Peninsula, Alaska (Robert Pegau, personal communication to Roseneau, 1973). Another unverified observation of Gyrfalcons wintering on Kharlov Island (which is an area where they breed) was made by Kraftanovski (cited in Dementiev and Gortchakovskaya 1945).

Sightings of single Gyrfalcons in Alaska during the winter have been reported more frequently than wintering pairs (Sheldon 1909, Gabrielson and Lincoln 1959, Irving 1960, Platt 1976). Roseneau (personal communication, 1979) received reports from Pegau of single birds on the Seward Peninsula during all months of the winter. He also observed

the tracks of at least one individual in the snow at a nest-cliff perching area. This particular nest-cliff was occupied by a successful pair of Gyrfalcons both before and after his winter observations (1970 and 1971). Observations of single falcons in areas of nesting habitat do not exclude the possibility that pairs of birds inhabited the area, and some of the observed singles actually may have been paired.

Nesting Behavior

Courtship and Pairing

Successful pairing in raptorial birds is the result of recognition of successive signals and displays performed during courtship. Size dimorphism (Snyder and Wiley 1976), female dominance (Newton 1979) and aggressive behavior (Willoughby and Cade 1964) in the genus Falco underscores the need for ritualized and nonaggressive postures that are recognized by the male bird during mate selection. Without signals permitting social communicaton, mating might not be successful without injury to one of the birds.

Despite the importance of the development of behavioral expressions during the pre-nesting period, the courtship behavior of wild Gyrfalcons is poorly known. Data from wild pairs are difficult to obtain because the entire courtship period occurs early in the breeding season when the arctic is generally inaccessible to most observers. Behavior of

captive Gyrfalcon pairs resembles that of the Peregrine Falcon (L. G. Swartz, personal communication, 1975); however, it has been necessary to be cautious when applying the behavior observed in captive pairs to the behavior used by wild pairs. Captivity may exaggerate or eliminate some types of behavior (Wrege and Cade 1977).

Platt (1977) described the courtship of captive and wild Gyrfalcons. He included descriptions of aerial and ledge displays performed by breeding pairs.

Wrege and Cade (1977) described thirteen displays that were common to the courtship of large North American falcons and named six vocalizations used by Gyrfalcons. When possible, the terminology given by Nelson (1970, 1977), Platt (1977) and Wrege and Cade (1977) has been used to describe the courtship activities observed in the present investigation.

Cliff occupation, aerial displays, ledge displays and food transfers between Gyrfalcons were observed during the pre-incubation period of reproductive activities. Not all of the courtship behaviors performed by Gyrfalcons were observed because of the inability to be present when some types were being performed. Nevertheless. the present observations have added to the scant knowledge of early season behavior.

Cliff Occupation

Cliff-nesting raptors use three patterns of nest-cliff occupancy: 1) pairs may remain on their territories throughout the winter, 2) only males may remain on territories throughout the winter and attract mates (or their mates return) during the spring, and 3) both sexes vacate the territory during the winter and return (usually males first) the following spring (Newton 1979). Gyrfalcons use all three of these patterns of cliff occupation, but overwintering of pairs and single males on nesting territories probably are the typical methods used to secure nesting cliffs. Even though Gyrfalcons are one of the first species to nest in the arctic tundra and alpine-tundra environments of Alaska, Common Ravens (Corvus corax) probably compete with the falcons for nest sites (White and Cade 1971; personal observation, 1976). Regardless of the nesting relationships between these two species (i. e., ravens creating nest sites suitable for later use by Gyrfalcons, Roseneau 1972) most nest sites used by Gyrfalcons in the Alaska Range were occupied every year. The low incidence of consecutive yearly nest site and nest-cliff occupancy typical of the Seward Peninsula (Roseneau 1972) and the North Slope (White and Cade 1971) apparently did not occur in the Alaska Range.

This may be the result of a combination of several factors. Fewer nest-cliffs per unit area are found in the Alaska Range, which may restrict pairs to fewer alternate nest-cliffs. Also, annual fluctuations of prey species are probably less extreme and changes in composition are less dramatic in interior Alaska than on the North Slope. The relative stability of prey populations in nesting areas enables Gyrfalcons to nest successfully. Although there are few observations, the paucity of nesting cliffs and moderated prey abundance may allow Gyrfalcons to make yearly use of traditional nesting cliffs.

The apparent displacement of a large group of Common Ravens was observed at a historical Gyrfalcon eyrie during early April, 1976. When first observed (11 - 12 March), the nest-cliff was being used as a roost by approximately 25 ravens. The large number of ravens were attracted to the area as a result of garbage produced by a nearby pipeline construction camp. During the day, the cliff was vacant while the ravens foraged at the camp dump. During the evening, the ravens would fly to the cliff to roost. Gyrfalcons were not present at the cliff at this time.

Twenty-four days later (5 April) ravens were still present at the camp dump. When the nest-cliff was examined during the afternoon and evening hours that same day, ravens were not present but a pair of Gyrfalcons was perched near the summit of the cliff. Instead of using the cliff for

roosting, ravens at the dump flew to a soilbank across the valley to roost. Although unwitnessed, the Gyrfalcons apparently had displaced the ravens from roosting on the nest-cliff.

Egg laying by this particular pair of Gyrfalcons commenced during 20 - 25 April. Thus, cliff occupation probably occurred 3 - 6 weeks prior to the initiation of egg laying. This period of cliff occupancy was shorter than that generalized by Platt (1977), but allows enough time for the 14 day folicle development that has been known to occur in captive female falcons (Swartz, personal communication, 1975; Nelson 1977). Cliff occupancy, in this case, may have occurred when the pair bond became sufficiently strong or when the territorial defense of the pair became developed enough (at the onset of breeding) to cause the falcons to challenge the ravens that were occupying the nest-cliff.

Following the appearance of Gyrfalcons at the nest-cliff, courtship behavior was performed by this pair. These activites included aerial flight displays, food transfers, mutual ledge displays and vocal exchanges between the pair.

Another example of sudden occupancy of a nest-cliff was observed in 1976. During surveys in March and April, a single male Gyrfalcon was located at a cliff previously used for nesting. The male was always responsive and slightly defensive of the nest-cliff when the nest-cliff was inspected. This male used 'prominent perching' behavior to

announce his presence and presumably to attract a mate (Nelson 1974); however, aerial advertisements or aerial displays were not conducted in March and April. The last observation of a single male was made on 22 April.

When this cliff was next observed on 4 May a pair of Gyrfalcons was in residence. Surprisingly, the female was incubating a clutch of three fertile eggs. The male may have secured his mate during the 12 day lapse in observations. Back-dating from hatching suggested the female spent the latter half of that 12 day period laying eggs (approximately 48 hours/egg, Platt 1977). The sudden appearance of the female Gyrfalcon was difficult to explain because the normal events of courtship, copulation and 'egg laying lethargy' cannot be reasonably condensed into a period of six days (Olendorff 1968, Cade et al. 1977). Although the male Gyrfalcon at this cliff appeared not to be mated throughout my last observation in April, his lack of aerial displays and the egg laying phenology of the female suggest that he was mated and that the female was not seen.

At the same time, the disappearance of a Gyrfalcon of unknown sex was observed from a nest-cliff located 18 km from the pair described above. It is purely speculation, but possible that this Gyrfalcon was the mate of the male at the nearby location. The fact that this bird did not remain at its' nest-cliff might suggest that it was a female

bird. Platt (1977) noted that unmated male Gyrfalcons more commonly occupy cliffs through the spring and summer, although unmated individuals of each sex have occupied nest-cliffs throughout the nesting season.

Aerial Flight Displays

Aerial flight displays are one of the first courtship activities performed by male falcons. Aerial display serves two functions: advertisement for a mate and announcement of occupancy of a nesting territory (Newton 1979). Aerial flights are probably used because they communicate these signals over long distances. Among Gyrfalcons, aerial displays of males begin early in the nesting season. Males present at nesting cliffs during the winter would be able to perform early advertisement.

Platt (1977) described three aerial courtship displays (undulating roll, eyrie fly-by, and mutual floating) performed by Gyrfalcons. These types of flights were not observed in this study, but two additional displays were recorded that were not described by Platt. Male soaring and mutual soaring were performed by a pair of Gyrfalcons on 10 April, prior to the time of egg laying (20 - 25 April). Additionally, during incubation and rearing of young, eight male soaring flights and three mutual soaring flights were observed. All soaring flights were seen on nine different days between 10 April and 5 July (Table 1). Other aerial

Table 1. Soaring flights of Gyrfalcons in Alaska.

Date	Type	Duration, min	Nesting Phenology
10 April	male soaring	10	courtship
5 May	male soaring	5	incubation
26 May	male soaring	5	incubation
26 May	male soaring	6	incubation
27 May	male soaring	2	incubation
1 June	male soaring	1.5	incubation
3 June	male soaring	3	incubation
4 June	male soaring	3	pipping
4 June	male soaring	4	pipping
		$\bar{x} = 4.4 \pm 2.6$	
10 April	mutual soaring	45	courtship
1 June	mutual soaring	2	incubation
3 June	mutual soaring	2	incubation
10 June	mutual soaring	4	nestling (5 day)
5 July	mutual soaring[1]	80	nestling (30 day)
		$\bar{x} = 26.6 \pm 35.0$	
		$(\bar{x} = 13.3 \pm 21.2)^2$	

[1] Soaring behavior on this occasion was similar to display flights but it is unlikely that this was an aerial display. This soaring event occurred on a very windy day that was conducive to soaring flight.

[2] Excludes 80 minute flight on 5 July.

displays might have occurred but went unrecorded because intensive observations began after incubation was underway.

During the pre-egg laying period the soaring activity of Gyrfalcons occurred 30 - 200 m directly above the nest cliff or eyrie. No flights ended with advertisement of the nest site (i. e., landing at the nest site) as has been described for the aerial flights of Gyrfalcons (Platt 1977), Peregrine Falcons (Nelson 1970) and Prairie Falcons (Enderson 1964). Soaring displays (either solitary or mutual) were different from other aerial displays because soaring did not involve diving, quick aerial manuvers, vocal exchanges, or eyrie advertisement that are characteristic of other falcon displays.

Male soaring was first observed on 10 April 1976. The male soared in circles above the nest cliff without flapping its wings (similar to a Buteo type hawk). Occasionally the male would remain nearly motionless, except for slight movements of tail and wings, while soaring above the nest-cliff. Diving or other types of quick flight were not observed. Changes in altitude occurred as slow, deliberate manuvers, usually by quartering into or away from the wind.

Mutual soaring was the same as male soaring except that it included participation by the female. A pair of Gyrfalcons engaged in this activity above a nest-cliff on 10 April 1976 (prior to egg laying). The female began soaring about 30 minutes after she received prey from the

male. Immediately, the male Gyrfalcon joined with soaring flight. No vocal exchanges were heard during the 45 minute observation period. The female followed the flight path of the male and remained separated by 2 - 20 m. All flight was roughly level and produced 'circles' varying from 50 - 200 m in diameter. When soaring on a large diameter the pair sometimes separated and each bird proceeded in its own elevation and curvature of flight. If the separation distance was great, the female re-joined the male by soaring directly toward him, and resumed following the male.

Mutual soaring was unlike Platt's mutual floating display because mutual floating involved a slow descent by the pair, each having its tail spread, legs down, and wings partially closed. During floating displays the female gave the defensive 'kekk' call. In contrast, soaring displays were characterized by nonvocal birds flying with their legs up, wings fully extended, and tails usually closed.

The length of soaring flights decreased during incubation. The last male soaring flight was on 4 June (one day before hatching) and the last mutual soaring display occurred on 10 June (5 days after hatching). Although soaring activity was not observed during the early phases of courtship and its value in mate attraction cannot be assessed, the decrease in this activity during incubation suggests that the display serves as announcement of occupancy of the nesting territory. Such flights were not

necessary when competition for nesting cliffs had ceased. The observation of a soaring flight when the young were 30 days old probably reflected the use of non-flapping flight induced by weather conditions. Recently fledged Gyrfalcons in a nearby area were also observed soaring under similar conditions (at a later date).

Incubation

Raptors may be divided into three categories based on the participation of males in incubation (Newton 1979). Males may fail to incubate, provide partial relief (especially while females were eating) or share equally in incubation. Falcons, like most birds of prey, follow the pattern of males providing partial participation in incubation. However, in some species (e. g., Merlin Falco columbarius, Peregrine Falcon and Gyrfalcon) males incubate for as much as one third of the daylight period (Enderson et al. 1973, Platt 1977, Newton et al. 1978, Newton 1979). In many raptors separation of roles or activities by sex is characteristic throughout the breeding season. Among Gyrfalcons, this separation of roles may be the greatest during incubation.

To illustrate the sex related roles of Gyrfalcons the following behaviors of incubating falcons are examined: 1) the duration of parental shifts, 2) changes in position/posture of incubating birds and 3) hunting activity

during the incubation period. The definitions of incubation activities are given by Nelson (1970):

> 1) nest relief - a change-over of incubation duty from one adult of the pair to the other.
>
> 2) parental shift - the period between two nest reliefs when one of the parents tends the eggs. A parental shift may be subdivided into sitting spells.
>
> 3) sitting spells - periods of uninterrupted incubation, the break in contact between eggs and brood patch being the criterion used.
>
> 4) standing spells - these occur especially in warm weather, when the adult may stand over the eggs. In the Peregrine there is a gradual transition from the sitting position, in which incubation is most effective, and the standing position in which the adult appears only to be shading the eggs.
>
> 5) breaks - the short periods spent off the eggs by the parent whose shift it is.
>
> 6) recesses - the periods of off-duty enjoyed by the bird who is presently relieved of incubation duties.

Incubation activities were observed at one Gyrfalcon eyrie in 1976. Between 3 May and 5 June, incubation events were recorded on 16 days during 112.4 hours of observation. These observations occurred between 0615 and 2200 hours and varied from 1.3 to 15.5 hours in length (Figure 2). During these observations 10 parental shifts were timed (Table 2). Another 11 parental shifts, although timed, were of minimum

Table 2. Length of parental shifts during incubation by Gyrfalcons in the Alaska Range, 1976.

	known shifts (hrs)				incomplete shifts (hrs)				all shifts (hrs)			
Sex	n	$\bar{x}$	Σx	%[1]	n	$\bar{x}$	Σx	%[1]	n	$\bar{x}$	Σx	%[1]
male	4	0.11	0.43	5.7	-	-	-	-	4	0.11	0.43	0.8
female	6	1.18	7.11	94.3	11	4.21	46.31	100	17	3.14	53.42	99.2
TOTAL	10	0.75	7.54	100.0	11	4.21	46.31	100	21	2.56	53.85	100.0

[1] Percent of total hours of incubation by each sex.

length because the birds were incubating either before observations began or after the blind was left.

Behavior of Incubating Adults

The behavior of falcons includes a variety of activities performed by adults as they incubate their eggs. Nelson (1970, 1977) thoroughly described the behavior of Peregrine Falcons during incubation. Platt (1977) described the behavior of incubating Gyrfalcons.

Commonly, the behavior of incubating birds includes numerous settling movements performed by adults as they reposition themselves above the eggs. Drent (1973), in discussing the natural history of incubation, showed that these movements influence the position of the egg. A stable egg position (with respect to rotation) is maintained throughout incubation and the actions of the adult tended to turn eggs that had rotated from the optimal position.

During 30.2 hours of female incubation, data were collected on the settling movements of Gyrfalcons. Movements included rising, standing above eggs, turning to face a new direction, rousing (ruffling and resettling of feathers), shuffling of feet, 'head throwing' (Platt 1977) or 'rocking' (Nelson 1970) and wing pumping (investigator's terminology). These activities interrupted periods of quiet incubation often characterized by dozing, erection of lower-back feathers, preening and snapping at insects. Nelson

(1977) noted that the movements of the incubating bird ensured that the eggs were in contact with the brood patch.

One distinctive behavior was 'head throwing' (Platt 1977) or the combination of 'rocking, chest-dropping, arching, leveling' (Nelson 1970). In this study it was found that settling movement followed any rising, standing or rousing of the parent bird. When repositioning itself on the eggs the falcon pumped its head upward (bill pointing downward), usually twice in rapid succession. The posterior body was pressed close to the nest as the chest and head were lowered to the normal incubating position. This manuever was often repeated once or twice before a stable incubation posture was maintained.

The female was observed to pump her wings several times, in a rowing fashion not unlike the thrusting of the wings common during scraping activities, as a conclusion to the above sequence of events. The significance of this behavior was unknown and it has not previously been described as a normal settling movement in falcons.

Table 3 (and Figure 3) shows the time elapsed between settling movements of incubating and brooding Gyrfalcons. These observations were made on eight different days during late incubation, hatching and early brooding activity. The mean time between movements during incubation decreased from 0.45 hours on 1 June to 0.15 hours on 4 June. The shortest time period between settling movement was less than

Table 3. Female Gyrfalcon settling movements during late incubation, hatching and early brooding stages, 1976.

Phenology	Date	Time: Begin Observation	Time: End Observation	Shift length (hrs)[1]	Number of settlings	Mean time between settling (hrs)[1]
incubation	1 June	0730	1029	2.98	4	0.45
incubation	1 June	1151	1202	0.17	1	0.18
incubation	2 June	1420	1512	0.87	3	0.25
incubation	2 June	1518	1656	1.63	1	0.56
incubation	3 June	0825	1124	2.98	13	0.18
incubation	3 June	1350	1515	1.42	3	0.03
incubation	4 June	1016	1044	0.47	1	0.15
hatching	5 June	0651	0809	1.30	8	0.15
hatching	5 June	0811	0827	0.25	2	0.10
hatching	5 June	1108	1248	1.67	6	0.25
hatching	5 June	2320	2400	0.66	2	0.27
hatching	6 June	0524	0701	1.62	6	0.22
hatching	6 June	0755	0936	1.68	4	0.18
hatching	6 June	11.15	1703	5.80	26	0.20
hatching	6 June	2115	2358	2.71	10	0.26
brooding	7 June	1004	1115	1.18	3	0.10
brooding	7 June	1444	1518	0.57	4	0.11
brooding	7 June	1545	1601	0.27	1	0.12
brooding	7 June	1620	1628	0.13	1	0.08
brooding	7 June	2014	2139	1.42	8	0.15
brooding	8 June	0710	0737	0.45	4	0.09
				30.23	111	

[1]Hours and hundreths of hours.

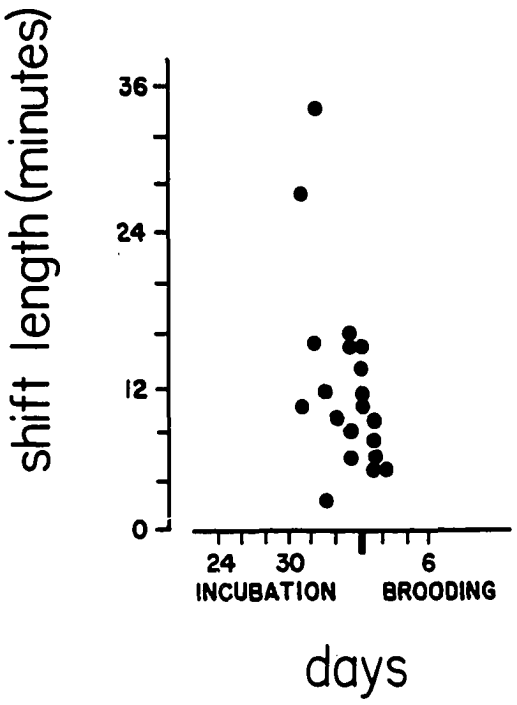

Figure 3. Length of incubation and brooding shifts of a female Gyrfalcon in the Alaska Range.

0.1 hours on 3 June. The time between settling movements decreased as hatching approached (Figure 3). During hatching the frequency of movements continued to increase. This change in pattern of settling movements may be used as a measure of the stage of incubation, especially as hatching approaches.

Settling movements were not recorded when the male was incubating so a comparison of the frequency of movements by the male and female was not possible. The male's role in incubation was so minimal that the behavioral contribution to settling movements and activities was virtually insignificant.

Nest relief was another activity that showed behavioral interaction among the pair of falcons. Most relief occurred when the mate (male) returned to the area of the nest. Seven female shifts ended when the male returned with prey and transferred it to the female. Unlike the 'food transfer-nest relief' sequence of Peregrine Falcons (Nelson 1970, 1977) where the male incubated while the female was eating, the male was observed to perch near the nest or soar above the nest-cliff after food transfers were made during the incubation period. The mean length of time the eggs were left untended after the female left the nest was 4.5 ± 3.1 minutes ($n = 4$). The longest recess was eight minutes and it occurred when the female ate an arctic ground squirrel (Spermophilus parryi) near the nest.

Not all female shifts ended when the male returned with prey. The male arrived at the nest rim without prey on one occasion and, after the female departed, the male began incubating. On another occasion, two days before hatching, the female left the nest to soar above the nest-cliff. The male joined the female and together they soared for approximately 10 minutes. During this time the sky was clear and the eggs were exposed to the sun so there was little danger of excessive cooling of the eggs. Also, ambient temperatures were low enough to prevent overheating of the eggs. The female returned to the nest after the male departed the nest area. On other occasions, the female ended incubation by pursuing intruders that were seen from the nest. The female defended the nest when Golden Eagles (Aquila chrysaetos), Long-tailed Jaegers (Stercorarius longicaudus) and red foxes (Vulpes vulpes) passed near the nest.

Parental Shifts

It was found that the female Gyrfalcon incubated almost exclusively, both during the daylight (94.3 %) and nightime hours. However, only one observation of the female incubating through the night was obtained. Males conducted very little incubation during the day or night. The percent day-time shift of females was longer than the shifts reported by Platt (1977, females 67 %) and for Peregrine Falcons by Enderson et al. (1973, females 60-70 % depending

on stage of incubation). Two factors may help explain this observed difference: 1) Incubation was not observed at all times of the day, nor were the observed times viewed with equal intensity. It is possible that the discontinuous nature of the observations biased the results obtained during incubation, thereby exaggerating the role of the female. 2) The longer female shifts in the observed pair may be the result of individual variation in participation in nesting activities.

Incubation shifts of known length differed by sex (Figure 4). The male incubated for a mean shift of 0.11 hours and the female incubated for a mean shift of 1.18 hours. The male incubated only during the time the female ate prey that she received during food transfers from the male. The short male shifts reflected the time required for female feeding. When finished eating she returned to the nest and then the male would leave.

A total of 11 female shifts were observed that were of minimum duration because they were not observed to completion. These shifts averaged 4.21 hours and were 3.5 times the mean length of known shifts (Table 2). Platt (1977) found that the shifts of female Gyrfalcons averaged 4.3 hours during complete sessions and 3.5 hours when sessions were not fully observed. The latter values were comparable to the minimum shift lengths observed in this study. Platt's shifts of known length were much longer than

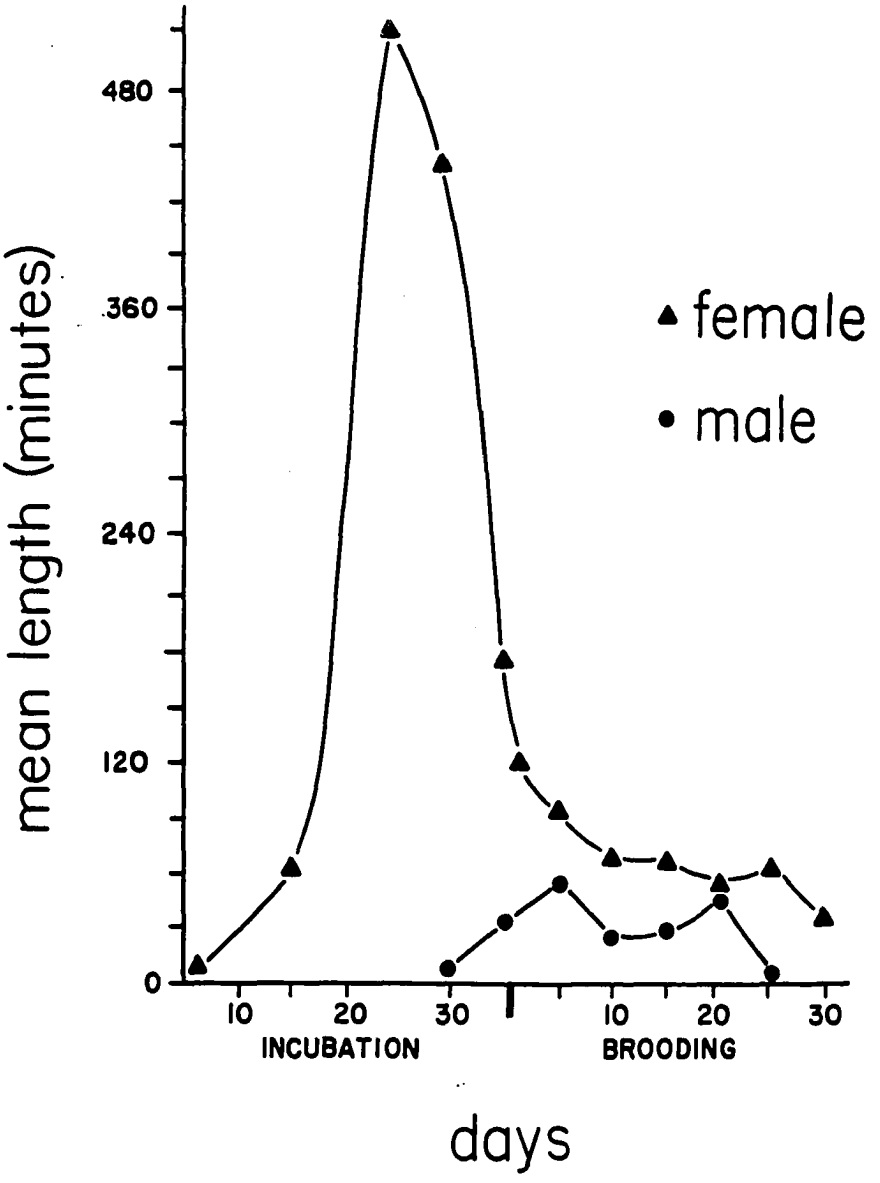

Figure 4. Mean length of incubation and brooding shifts of a pair of Gyrfalcons in the Alaska Range.

the female shifts which were observed completely in this study. The discrepancy may have resulted from the possibility that shorter incubation shifts were more likely to be observed to completion than long incubation shifts, if continuous observations were not maintained. Enderson et al. (1973) using time-lapse cameras (continuous observation) found that the mean shift length for female Peregrine Falcons was 4.1 hours. Continuous observations of incubation in Gyrfalcons were not available for comparison.

The shortest female shift was nine minutes and began when the female returned to the nest after eating. It ended when the female left the nest to defend it against a Golden Eagle. The longest female shift was not observed to completion, but included at least 8.5 hours of incubation without interruption. This shift occurred 26 days after the initiation of incubation. The length of female shifts decreased as the time of hatching approached (Figure 4).

Male incubation shifts were observed only four times (Table 2). All shifts were completely timed. The longest shift lasted 17 minutes and it ended when he left the nest abruptly, apparently in response to an intruder. The female reoccupied the nest after the eggs were unattended for less than 6 minutes. The shortest male shift was less than one minute. In that case, the male ended the shift by soaring above the eyrie. The soaring activity lasted about two

minutes and subsequently the male disappeared. The female reoccupied the nest while the male was soaring.

The male took a greater role in incubation as hatching approached (Figure 4). During the last five days of incubation the male incubated for more time than he did during the first 30 days of incubation. This increased interest in the nest continued until the nestlings were 5 days old. Computed on the basis of the total incubation and hatching periods, the male incubated for less than 0.1 % of the total time, but during hatching he brooded for 7.7 % of the time. After hatching, the male brooded less than 1.0 % of the time.

Nestling Period

In raptors the roles of the parents are different during the early nestling period but tend to merge as the female begins hunting during the late nestling period. When nestlings are present, the male hunts for prey to provide to the female and/or nestlings. In most species the male is seldom seen near the nest unless it is returning with prey to transfer to the female or young. Sometimes the male feeds or broods the young, but these activities generally are the responsibility of the female. During the nestling period the duties of the female gradually change as the needs of the developing young change. Newton (1979) noted

three phases of female behavior: 1) continuous brooding except during time of feeding; 2) intermittent brooding, perching near the nest and feeding the young; and 3) development of hunting activity during long absences from the nest and little feeding of the young. During the last phase the activities of the female are more similar to those of the male.

These general characteristics of adult behavior during the nestling period apply to the Gyrfalcons in this study. Brooding, feeding and food caching activities are discussed in this section. Hunting activity throughout the nesting season is discussed in a later section.

Brooding

Brooding behavior includes an assemblage of activities performed by adults to protect young chicks from chilling or overheating especially before the chicks attain thermoregulatory control. Protection from excessive cooling is most important during early nestling life because hatching occurs when ambient temperatures are low. Later, protection from overheating is more important because the young are exposed to direct sunlight of sufficient intensity to possibly cause death (Fyfe and Olendorff 1976).

Table 4 lists the brooding sessions of a male and female Gyrfalcon during hatching (5 - 6 June) and post hatching (7 June - 2 July) periods in 1976. Eighty sessions

Table 4. Length of brooding sessions by sex in Gyrfalcons, Alaska Range, 1976.

	Hatching, 5-6 June											
	known sessions				incomplete sessions				total sessions			
		Hours[1]				Hours[1]				Hours[1]		
Sex	n	$\bar{x}$	Σx	%[2]	n	$\bar{x}$	Σx	%[2]	n	$\bar{x}$	Σx	%[2]
male	6	0.55	3.30	35.3	1	0.41	0.41	1.9	7	0.53	3.71	11.9
female	3	2.02	6.05	64.7	11	1.94	21.35	98.1	14	1.96	27.40	88.1
	Post-Hatching, 7 June - 2 July											
male	10	0.51	5.15	10.0	4	0.92	3.69	14.5	14	0.63	8.84	11.8
female	47	0.94	44.18	90.0	17	1.28	21.79	85.5	64	1.03	65.97	88.2
TOTAL	66	0.89	58.68	-	33	1.43	47.23	-	80	1.32	105.92	-

[1]Hours and hundreths of hours.

[2]Percent of total hours of brooding by each sex during hatching and post hatching categories.

were observed, however 33 were of minimum length because they were not observed to completion or the sessions were in progress when observations began. During hatching the male brooded for 35.3 % of the known sessions but the proportion was only 11.9 % when observations of minimum length were included. For all classes of observation the female brooded more often than the male. The male ended brooding five days earlier than the female.

The mean length of brooding sessions also differed by sex (Table 4). During hatching the mean brooding sessions of the female ($\bar{x}$ = 2.02 hours) were approximately four times longer than those of the male ($\bar{x}$ = 0.55 hours). In the post hatching period the difference was not as great, but brooding sessions by the female ($\bar{x}$ = 0.94 hours) were longer than those of the male ($\bar{x}$ = 0.51 hours).

The last episode of brooding (shading) occurred when the young were 27 days old (2 July). This lengthened the estimates of brooding periods reported by Jenkins (1974, 1978) and Platt (1977) by nearly one week. The more southerly latitude of the study area may have explained the observed difference. All observations of late stage brooding sessions involved shading the young from exposure to direct sunlight. Weather records from the base camp located 1.2 km from the eyrie showed that maximum daily temperatures ranged from 24 - 28° C. during the last week of brooding. Previous maximum daily temperatures ranged

from 11 - 20° C. The increased temperature and the associated clear sky during the fourth week of nestling life probably caused the extension of the brooding period.

On calm, sunny days the nestlings panted and gave distress vocalizations if they were not being shaded by the adults. Adults shaded the chicks with drooped wings to maximize the shadow area. During the late-stage brooding, the large size of the young prevented all of them from being shaded at the same time. Under these conditions the young falcons rotated their positions because the unshaded one(s) eventually displaced the ones being shaded.

Brooding in direct sun caused panting and feather erection in the adults. Despite risking becoming overheated, the adult placed its dark colored back or side toward the sun. The shading posture of Gyrfalcons was similar to that of Peregrine Falcons (Enderson et al. 1973). This posture not only created the largest shadow surface for shading but also increased heat reception in the adult.

Feeding

The feeding of young was the major nest site activity performed by the adults during this phase of the nesting cycle. Both adults fed the young; however, as in most species of raptors, females did most of the feeding. Jenkins (1974) identified two types of feeding behavior: feeding (the act of ripping morsels of food and offering them to the young) and food-bringing (leaving prey at the

nest for young to consume themselves). Both behaviors were observed, but the male did more food-bringing and less feeding than the female. As the chicks grew older prey was more commonly dropped at the nest rim. After fledging, prey was transferred from the adults at the eyrie or at nearby perches. Aerial transfers of prey between adults and fledglings probably occurred but none were observed during this study.

Feedings and deliveries of prey at the study eyrie were observed 111 times between 5 - 10 June 1975 and 5 June - 20 July 1976. Figure 5 shows the times when these activities were performed by the male and female. In 1976, the first time the female used food-bringing occurred when the young were 27 days old, although direct feedings continued until the young were 44 days old. Food-bringing activity by the female increased during the late nestling period but did not replace feeding activity.

Normally the male did not feed the young directly, but delivered food to the female or, on occasion, to the nest rim. On the few occasions when the male fed the young, the female arrived at the nest and displaced the male and then continued the task of feeding the nestlings. This was observed when the young were 9, 18, 25 and 29 days old (Figure 5). Twice, when the nestlings were 27 and 28 days old, the male fed the chicks immediately after the female departed the eyrie after she had ended a feeding session.

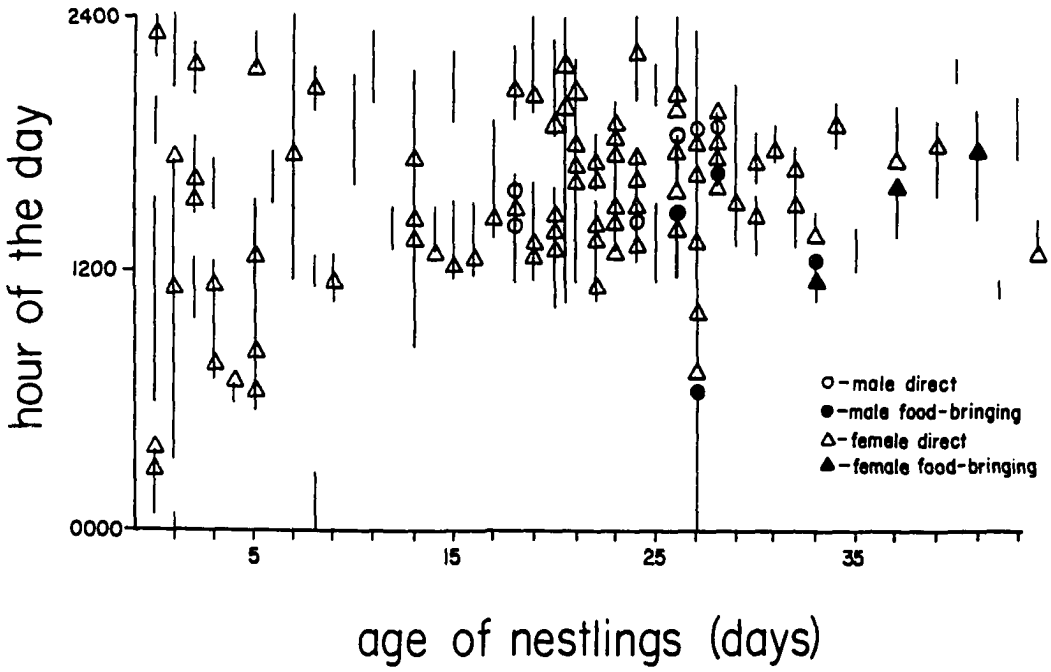

Figure 5. Daily feedings of nestling Gyrfalcons in the Alaska Range, 1976.

In general, male food-bringing replaced direct feeding of the chicks during the late nestling period.

Figure 6 shows the distribution of feeding/food-bringing events throughout the day. Feedings were not observed at all hours of the day, although observations were not made at all times of the day. Jenkins (1974), studied a nest located north of the Arctic Circle and used continuous time-lapse photography to document feedings at all hours of the day. The discontinuous nature of the observations in this study probably left some feeding periods unrepresented. The high correlation ($r = 0.83$) between the distribution of percent hours observed and number of feeding visits has suggested that unequal hourly observations contributes to the apparent absence of feeding during some hours of the day (Figure 6A, B).

Alternatively (if feedings were expressed per hours of observation), the low number of feedings that occurred between 2300 - 0200 ADT may be the result of darkness (Figure 6C). Even though Dementiev (1960) and Kistchinski (1957) have attributed good twilight vision to Gyrfalcons, Fox et al. (1976) have shown that visual acuity and resolution in the American Kestrel, Falco sparverius, falls markedly with decreased light intensity. Since the study area lies south of the Arctic Circle, continuous daylight does not occur during the nesting season. The longest days of summer (20.5 hours of sun above the horizon) have short

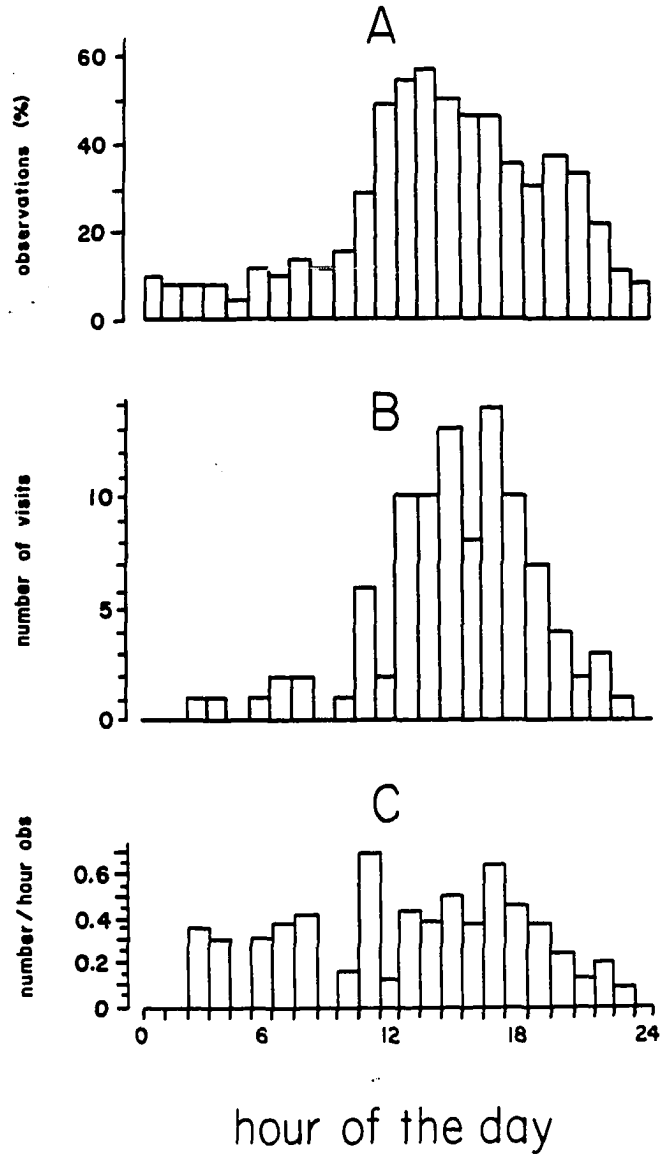

Figure 6. Hourly distribution of feedings of nestling Gyrfalcons in the Alaska Range, 1976.

A. Percent of the entire nestling period observed.
B. Number of feeding and food-bringing events by the hour.
C. Number of feeding events per hour of observation.

periods of considerable darkness, especially when clouds are present, which may prevent Gyrfalcons from hunting successfully during these times. Before and after the summer solstice day-lengths are even shorter. Therefore, feeding during the early and late nestling period is restricted by longer periods of darkness (Figure 2). The decreased activity of diurnal prey species during darkness may also decrease the success of Gyrfalcon hunting.

Maximum feeding and food-bringing activity occurred between 1100 - 1800 hours ADT at the nest site studied in 1976 (Figure 6). This peak of activity was similar to the distribution of feeding visits given by Jenkins (1974).

The rates of feedings of nestlings per 72 hour age-class have been given in Table 5. Average feedings per nestling per day ranged from 0.8 when the young were one week old to 4.8 when the young were nearly four weeks old. The number of feedings per nestling per day gradually increased as the chicks became older. Enderson et al. (1973) found the number of daily feedings of nestling Peregrine Falcons increased only after the first few days, and then remained stable. Jenkins (1974) did not compute the frequency of feeding for Gyrfalcons, but he listed a maximum of six feeding and/or food-bringing events per day. In this study the maximum frequency was seven feedings per day.

Table 5. Feeding rates of nestling Gyrfalcons, 1976.

Age of young[1]	Number of feedings observed	Amount of age class observed (hrs) (%)	Average feedings/ nestling/ day[2]	Observed Time between feedings (min)	Time for each feeding (min)
0-2	8	44.66 (62)	1.43	158 ±193.0	10.8 ± 5.0
3-5	7	21.59 (30)	2.59	171 ±122.0	13.2 ± 4.9
6-8	2	20.33 (28)	0.79	-	7.0 ± 4.2
9-11	2	9.83 (14)	1.59	-	-
12-14	4	9.83 (14)	3.17	96 ± 73.5	15.2 ±12.1
15-17	5	25.99 (36)	1.54	-	9.7 ± 3.0
18-20	17	56.74 (79)	2.39	21 ± 20.8	9.7 ± 5.3
21-23	18	54.08 (75)	2.67	74 ± 52.2	7.1 ± 5.9
24-26	12	19.91 (28)	4.76	64 ± 51.2	8.6 ± 5.2
27-29[3]	20	37.92 (53)	3.14	71 ± 71.5	9.8 ± 6.5
30-32	4	11.74 (16)	2.08	-	9.3 ± 6.7
33-35[4]	7	9.75 (14)	4.17	76 ± 19.3	8.0 ± 2.0
36-38	1	7.25 (10)	1.11	73	8.0
39-41	1	3.84 (5)	2.22	-	35
42-44	2	8.00 (11)	2.02	38	-
45-47	1	2.50 (3)	3.70	-	-

[1] Beginning with the hatching of the first chick.

[2] Assumes equal probability of feeding during entire day.

[3] One captive-reared bird fostered into nest.

[4] Captive-reared bird fledged.

The male and female Gyrfalcon exhibited different behavior when feeding their young. Some differences probably result from the dominance of females, which is common in diurnal raptors (Wrege and Cade 1977, Newton 1979). During feedings of nestlings the male was not intimidated by the young as Platt (1977) has suggested. The following description of feeding behavior is based on 99 feedings by the female and 12 feedings by the male.

The female fed the young more deliberately than the male. After receiving prey from the male, the female prepared the prey for feeding at a perch away from the eyrie. For example, the tough skin of an arctic ground squirrel was ripped apart, but not removed, which assured access to the fleshy tissue during the quick period of feeding that followed. Sometimes the intestine and stomach of arctic ground squirrels were removed during the preparation period; at other times these parts were discarded at the nest during the feeding. Although close observations were not always possible when prey was prepared away from the nest, it did not appear that the female ate any substantial part of the prey. Usually, several minutes of rapid plucking of feathers or pulling of skin preceded delivery of the prey to the nest.

At the nest the female fed all young individually (two and three chicks observed in 1975 and 1976, respectively), rather than the most vocal and aggressive one(s). During the feeding, the prey was torn rhythmically and there was seldom any pulling of prey that did not yield a piece of meat for the young to eat. The routine of bowing, pulling, reaching and delivery of food was only interrupted when the young were not eating eagerly. When the young falcons slowed or stopped eating, the female used the 'chup' vocalization to induce them to resume eating (Wrege and Cade 1977). If the young did not respond, the female ate the piece of meat that was offered to the chicks.

Feedings by the male were less deliberate and were frequently interrupted by the female. When the female arrived at the nest (without prey) while the male was feeding the young, the male quickly relinquished the food and left. However, on one occasion when the male was feeding the young, the female arrived with additional prey. Both adults then fed the young simultaneously for several minutes. The male remained at the nest for an additional six minutes after finishing the feeding of the young.

Unlike the female, the one male which was observed seldom prepared food prior to arrival at the nest. In most cases prey items were transferred to the female away from the nest. One-half of the observations of the male with prey at the nest were episodes of food-bringing and one-half

consisted of direct feedings. During food-bringing the male dropped the prey at the nest rim and quickly departed. When feeding the young the male usually plucked prey on the nest rim while the young eagerly awaited being fed.

Platt (1977) claimed that the male Gyrfalcon was intimidated by the aggressive begging of the young. Thus, the quick food bringing exchanges at the nest by the male minimized contact with the young. Despite vocal announcement, in this study, arrivals at the nest by the male often occurred when the young were inattentive to the arrival. Once at the nest, the young responded quickly but did not mob the male. Also, the male did tolerate the young during the time when he directly fed them.

Male food-bringing behavior may maximize the time available for hunting by the male falcon. Efficient, quick transfers of prey at the nest (when the female was not available for receiving prey) minimizes the amount of time needed for feeding by the male. Even though the role of the male in feeding is minimal, some feeding of young by the male did occur.

The feeding behavior of male Gyrfalcons varies among individuals. Jenkins (1974) filmed a sequence of cooperative feeding of nestlings where the male first gave pieces of food to the female who then fed them to the young. Wayre and Jolly (1958) watched the male frequently feed four week-old young. In this study the male was observed feeding

the young simultaneously with the female. Most often, males did little direct feeding of young and all observers have recognized that the primary role of the male has been to provide prey to the female during the nestling period.

Food Transfers Between Adults

Food transfers between adult raptors occur regularly during the nesting season. Prey deliveries to females by males are a general characteristic of pair-forming behavior (e. g., Brown and Amadon 1968, Brown 1976, Newton 1979). Among Gyrfalcons, food transfers from the male to female probably begin during the early phases of breeding (Platt 1977) and continue until the fledging of the young (Jenkins 1974, Muir 1974, Platt 1977, Platt and Tull 1977). In captive Gyrfalcon pairs, food transfers began with early courtship activities. In wild pairs, aerial transfers of prey were observed several weeks before eggs were laid. Food transfers between adults were not recorded after the young fledged.

Four types of prey transfers have been described for Gyrfalcons. Transfers have taken place 1) at the eyrie, 2) at perches near the nest (Muir 1974, Platt 1977, Platt and Tull 1977), 3) when the male leaves prey on the ground for the female to find later (Muir 1974), and 4) as an aerial exchange between adults flying near the eyrie (Murie 1946, Cade 1960, Jenkins 1974, Platt 1977). The third type of transfer listed above may simply be a modification of a

transfer normally occuring between birds at perches. However, Muir (1974) gave a convincing description of this type of transfer.

A total of 59 prey transfers from the male to the female were observed in 1975 and 1976 (Table 6). Transfers at the nest edge were most numerous (n = 28), followed by aerial exchanges (n = 13) and transfers at perches (n = 6); 12 exchanges occurred at uncertain locations. These observations were scattered from 10 April to 20 July; however, most sightings were made after 1 June during the time following hatching. The observed values differ significantly from the expected distribution of equal use of all methods of transfer (Chi-square test: $X^2 = 17.81$, $p < 0.01$, $df = 3$).

The sequence of food transfer events was largely determined by the behavior and action of the female towards the male. Characteristically, the male wailed rapidly (for vocalization sonagram see Wrege and Cade 1977, Figure 3b) when returning to the nest cliff with prey. This vocalization served as an announcement of arrival. If the female responded quickly and flew toward the male an aerial transfer of prey was completed. If the female responded slowly, the male occasionally flew directly to the nest and transfered the prey to the female at the nest rim. At other times, the male flew to a perch and waited for the female

Table 6. Number and types of food transfers performed by Gyrfalcons, Alaska Range, 1975 and 1976.

Type of food transfer	Number observed 1975	Number observed 1976	First and last date of observation
aerial	2	11	1 June - 20 July
nest edge	3	25	10 April - 3 July
perches	1	5	3 June - 10 July
uncertain location	1	11	19 May - 17 July
TOTAL	7	52	10 April - 20 July

to arrive before transferring the prey. Alternatively, if the female was at the nest, the male sometimes waited a short time at a perch and then delivered the prey to the nest. If the female was not present when the male returned with prey, the male would either feed the young or drop the food at the nest for the chicks to feed upon themselves.

The female used a food transfer vocalization when she approached the male to take food. Wrege and Cade (1977) termed this call a 'chatter' and they believed that both sexes used the call. In this study it was found that the female began begging with a short series of wails followed by rapid slurred chattering during which the female assumed a submissive, head-bowed, posture. The male responded with sharp, emphatic and staccato-like 'chips'. In neither wild nor captive Gyrfalcons did the male use a 'chatter' vocalization during food transfers.

Once the female began vocalizing and was standing close to the male, she either reached for the prey held in the males' talons or received the prey from the beak of the male. If the female reached for the prey, the male either released it directly from his talons or he quickly took the prey in his beak and proceeded with a 'beak to beak' transfer.

Aerial transfers had the same vocal sequence but the movement of the birds was different because of the necessity of sustaining flight during the transfer. Aerial transfers

were observed less than 30 m above ground level. The female left the nest or perch and, wailing, flew directly upward to the male. The female followed directly behind the male for a brief moment before beginning the 'chatter' vocalization. When the female began begging, the male moved his head toward his feet and took the prey in his beak. Simultaneously, the female moved into a position directly below the male. The prey was released from the beak of the male and caught by the feet of the female as she executed a half-roll beneath the male at the time of the release. The distance between the male and female was usually less than one meter. The aerial transfer sequence of Gyrfalcons was very similar to the movements of Peregrine Falcons traced from movie film footage by Nelson (1970). Aerial transfers in Gyrfalcons were completed in approximately 1 - 2 seconds.

Some variations in the release of prey included transfers in which 1) the male released prey directly from the feet, and 2) the prey was released by the male when the female was approximately 5 m below the male. The latter may be similar to the 'dead drop' of Peregrine Falcons described by Sherrod (1979). The male was never seen to roll and present the prey to the female as described by Bond (1949), but only released the prey when the female was flying below the male.

Once the aerial transfer was completed, the female returned to a perch and either ate or prepared the prey for feeding (depending on the stage of nesting). No matter what stage of nesting, the male briefly flew above the nest-cliff, then perched for a few minutes before departing the nest-cliff, presumably on another hunting flight. Once, during incubation, the male changed this pattern by incubating while the female was off of the nest. After hatching of the young, the male did not go to the nest following an aerial transfer of prey.

All aerial transfers observed in this study were executed without error. This was contrary to the observation made by Jenkins (1974); he observed a pair that struggled during the aerial transfer and finally completed it on a talus slide used frequently for prey transfers. Perhaps some pairs were more skillful in aerial exchanges than other pairs. In this study (in both years) once the adults committed themselves to an aerial transfer of prey it was conducted flawlessly. Most aerial transfers occurred so quickly that it was easy to miss seeing the event. However, the vocalizations that accompany the flying maneuvers act as a signal of a transfer in progress.

Food Caching

Food caching behavior is common among predators and serves as a valuable adaptive strategy in predator survival (Curio 1972). Most raptors cache prey during the nesting

season (Newton 1979). This behavior is well recorded in falcons, notably in the American Kestrel (Tordoff 1955, Stendell and Waian 1968, Mueller 1974a), Merlin (Greaves 1968, Oliphant and Thompson 1976), captive Prairie Falcons (Oliphant and Thompson 1976) and the Peregrine Falcon (Brown and Amadon 1968, Nelson 1970). Among Gyrfalcons, it is a common nesting activity that has been previously observed by Wayre and Jolly (1958), Jenkins (1974) and Muir (1974).

Food caching is the deliberate removal of uneaten prey from the nest followed by deliberate 'hiding' of the prey near the nest (Jenkins 1974). Actually, there may be little hiding of the prey as cached items were often in plain sight when the falcon left the caching area. In this study caching areas were either within sight or hidden from the eyrie. Talus, scree, cliffs or vegetated slopes were used for caching as long as they were located less than 400 m from the nest site.

In wild Gyrfalcons, intense caching behavior began when the eggs hatched (Figure 7). A total of 28 food cachings were recorded and all but one of them occurred after the eggs hatched. Captive pairs of Gyrfalcons (personal observation, 1975 - 1977) and Peregrine Falcons (Swartz, personal communication, 1976) held for breeding purposes cached frequently during courtship and incubation, an

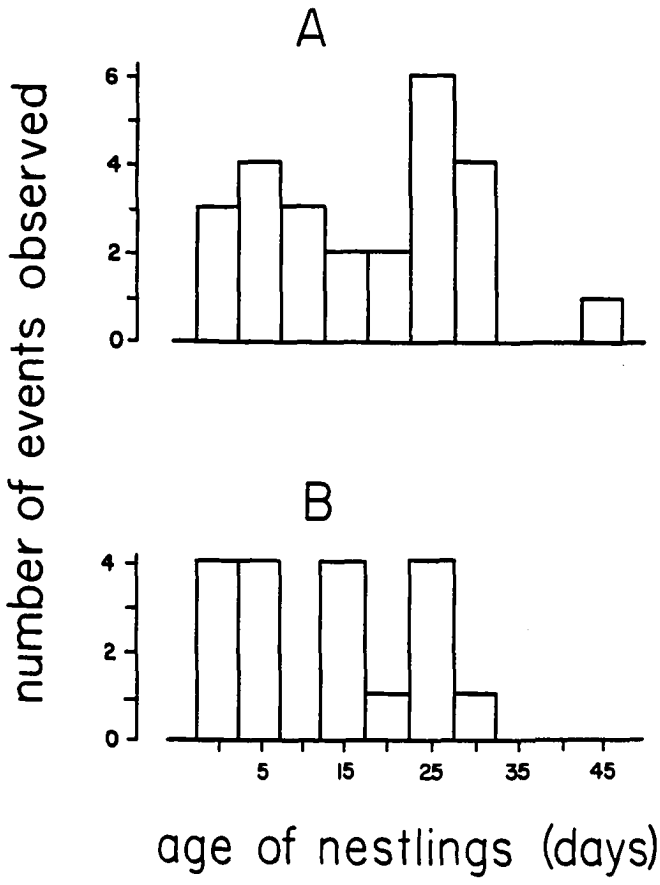

Figure 7. Caching and retrieval of prey by adult Gyrfalcons in the Alaska Range, 1976.

A. The number of food caching events observed.
B. The number of retrievals of cached prey observed.

observation that was not verified in wild birds. Nelson (1970) noted that wild Peregrine Falcons cached during the incubation and nestling periods but he stressed the adaptive strategy of this behavior because the primary prey (murrelets) were available only during their twilight flights. In this study, limited availability of diurnal prey probably did not influence the caching behavior of the adults.

Table 7 shows the types of caching areas used by Gyrfalcons. There was no significant difference in use of the caching areas (equal use of all types of caching areas, Chi-square test: $X^2 = 4.86$, $p < 0.10$, $df = 3$) among caching areas. The female conducted most of the caching (93 %), whereas the male made only a few caches (7 %). The caching behavior of a pair of captive Gyrfalcons was similar during three breeding seasons (1975-1977). Muir (1974) reported that both adult Gyrfalcons cached prey but he did not quantify the activity by sex. The lack of caching by male Gyrfalcons is contrasted by the caching behavior observed in wild Merlins and captive peregrines. Oliphant and Thompson (1976) found that the male Merlin cached prey and the female did not cache prey. Swartz (personal communication, 1979) noted that his male peregrine commonly cached prey yet the female of the pair cached prey infrequently.

Table 7. Prey caching activity of Gyrfalcons nesting in the Alaska Range, 1975 and 1976.

	Number of Observations	
Type of cache	male	female
talus slope	-	6
vegetated slope	-	6
rock cliff	-	11
uncertain	2	3
TOTAL	2	26

One observation of the male Gyrfalcon caching prey occurred when the female did not receive prey during an attempted transfer. In this case, the male returned from a hunting flight with an arctic ground squirrel and wailed to signal his presence for a food transfer. When the female, who was incubating tightly, did not leave the nest to meet the male, he stopped wailing and circled above the eyrie. In less than a minute he descended to one of the prey caching areas and returned without the prey. Although not directly observed in the act of caching, the circumstantial evidence suggests that the male cached the prey in the brief absence from the eyrie.

Prey caching in Gyrfalcons occurred either before or after part of the food was fed to the nestlings. Usually, prey remaining after feeding was cached. A total of 24 caching events were observed after the young were fed and only two caching events occurred before the nestlings were fed. Once, an arctic ground squirrel was cached before being fed to five day old young that had received a meal three hours previously. The second episode of caching before feeding was observed when a chicken (provided as supplemental prey) was taken directly to a cache at a time when the young were 27 days old.

Caching behavior continued through the nestling season. The last observed caching was made one day before the first

chick fledged (Figure 7). Maximum caching activity occurred when the young were four weeks old.

Retrieval of Cached Prey

Retrieval of cached prey for feeding to the young was observed 25 times (Table 8). This suggests a high use of cached prey. The female made 24 retrievals (96 %), whereas the male made only one retrieval (4 %). Retrieval of cached prey equaled or exceeded the number of observed cachings made during the same five-day period (Figure 7). Excess retrievals can be explained by the reuse of prey items that were not observed to be cached. Unfortunately, the time that elapsed between caching and subsequent reuse of individual prey items was not obtained.

Even though the male Gyrfalcon performed very few observed cachings (perhaps indicating few choices for reusing prey), he retrieved a partially consumed arctic ground squirrel on one occasion when the chicks were eight days old. On that day the male appeared at the nest-cliff without prey, flew to a caching area approximately 200 m from the nest and returned with prey for transfer to the female. The elapsed time of this event was not long enough for the male to have actively hunted. Roseneau (personal communication, 1979) observed a similar event on the Seward Peninsula when a male Gyrfalcon flew out of sight near a nest site and returned in minutes with a fully plucked ptarmigan. The duration of the absence and local conditions

Table 8. Retrieval and recaching of cached prey by Gyrfalcons in the Alaska Range, 1975 and 1976.

Type of Activity	Sex	Number of Observations		
		1975	1976	Total
retrieval	M	-	1	1
retrieval	F	4	20	24
recaching	M	-	-	0
recaching	F	1	5	6
TOTAL		5	26	31

did not allow enough time for active hunting and plucking activities by the male Gyrfalcon. These, I believe, may be the first observations of male Gyrfalcons using cached prey when normal hunting may have been unsuccessful.

Prey that was retrieved from a caching area was recached on six occasions when the prey was not fully consumed at the nest during the second feeding (Table 8). Recaching of prey was observed only when the chicks were less than seven days old. This behavior probably did not continue after this time because older nestlings fully consumed prey items during feedings. If food remained, recaching would have probably occurred regardless of the age of chicks. For example, Muir (1974) observed multiple recachings of the large bodied tundra hare (Lepus timidus) by Gyrfalcons whenever the hares were not fully consumed by the young falcons. Multiple recachings of prey did not appear to be common; instead they only occurred when large prey items were aquired or when the young were small enough to not require much food.

Hunting Activity of Adults

In raptors, hunting activity is greatly influenced by the stage of nesting and availability of prey. As the demand for food increases after hatching so does the hunting effort of the adults. Seasonal differences in the distribution, density, and vulnerability of prey species

also affects the hunting activity of nesting raptors. In most species, including Gyrfalcons, males provide most of the prey consumed by their mates and offspring. Females only begin leaving the nest area to hunt when the young are several weeks old.

Although the potential prey populations for Gyrfalcons in the Alaska Range were not measured or estimated, the diet of nesting pairs was determined by identifying the species present in prey remains and/or pellets collected at nest sites. The prey species found at three nesting locations are listed in Tables 9 - 11. These collections show that ptarmigan and arctic ground squirrels were the most important prey species of Gyrfalcons in the Alaska Range. The high frequency and biomass of arctic ground squirrels was similar to the incidence of ground squirrels found at other Gyrfalcon eyries in the Alaska Range (Murie 1946, Cade 1960).

Seasonal Use of Prey

Seasonal variation in use of prey by nesting Gyrfalcons is shown in Table 12. Remains of ptarmigan were present at all eyries during early collections and indicated that Gyrfalcons used them during the winter and early nest site selection or occupancy. In 1975, microtine rodents were taken as prey by one pair, but only when snow-melt was nearly completed. Microtines contributed little biomass as

Table 9. Prey remains found at 1975 study site, Alaska Range.

Prey Species	Number	% Frequency	% Biomass
Unidentified waterfowl	1	1.2	2.2
Ptarmigan, *Lagopus* sp.	35	43.2	48.4
Jaeger, *Stercorarius* sp.	1	1.2	0.9
Gray-crowned Rosy Finch, *Leucosticte tephrocotis*	2	2.4	0.2
Domestic chicken, *Gallus gallus*[1]	10	12.4	19.7
Unidentified small birds	5	6.2	0.3
TOTAL BIRDS	54	66.6	71.7
Arctic ground squirrel, *Spermophilus parryii*	14	17.3	25.6
Hoary Marmot, juvenile, *Marmota caligata*	1	1.2	1.4
Pica, *Ochotona collaris*	1	1.2	0.3
Microtine rodents	10	12.4	0.9
Unidentified small mammal	1	1.2	0.1
TOTAL MAMMALS	27	33.3	28.3
TOTAL PREY INDIVIDUALS	81	99.9	100.0

[1]Domestic chickens were provided as supplemental prey for the Gyrfalcons.

Table 10. Prey remains found at 1976 study site, Alaska Range.

Prey Species	Number	% Frequency	% Biomass
Unidentified waterfowl	1	0.6	0.9
Ptarmigan, *Lagopus* sp.	72	42.9	41.5
Unidentified large shorebird	3	1.8	0.9
Gray-crowned Rosy Finch, *Leucosticte tephrocotis*	1	0.6	<0.1
Unidentified small birds	17	10.1	0.4
Domestic chicken, *Gallus gallus*[1]	8	4.8	6.5
TOTAL BIRDS	102	60.7	50.3
Arctic ground squirrel, *Spermophilus parryii*	65	38.7	49.6
Microtine rodents	1	0.6	<0.1
TOTAL MAMMALS	66	39.3	49.7
TOTAL PREY INDIVIDUALS	168	100.0	100.0

[1]Domestic chickens were provided as supplemental prey for the Gyrfalcons.

Table 11. Prey remains found at a nearby nest site, Alaska Range, 1975 and 1976.

Prey Species	Number	% Frequency	% Biomass
Ptarmigan, *Lagopus* sp.	31	41.9	41.0
TOTAL BIRDS	31	41.9	41.0
Arctic ground squirrel, *Spermophilus parryii*	33	44.6	57.8
Mustelid	1	1.4	0.4
Microtine rodents	9	12.2	0.7
TOTAL MAMMALS	43	58.2	58.9
TOTAL PREY INDIVIDUALS	74	100.1	99.9

Table 12. Monthly use of prey by Gyrfalcons in

Month	Seasonal conditions	Nesting activity
April	winter	residence and/or cliff occupation and courtship
May	spring snow melt	incubation
June	spring	hatching, nestlings
July	summer	rearing nestlings
August	summer - autumn	fledging and dispersal
September	autumn	dispersal residence migration

the Alaska Range, 1975 and 1976.

Principal prey	Secondary prey
ptarmigan	-
ptarmigan	Arctic ground squirrel and microtines
Arctic ground squirrels	ptarmigan and passerines
Arctic ground squirrels	shorebirds and passerines
Arctic ground squirrels	ptarmigan
ptarmigan	waterfowl and migrant birds

prey and their use by Gyrfalcons may be the result of increased prey vulnerability during melting snow conditions or when populations are dense. Similarly, Kistchinski (1957) noted that Gyrfalcons on the Koliskiy Peninsula (Soviet Union) took Norway lemmings (Lemmus lemmus) during the period of high microtine visibility in the spring. Roseneau (1972) found low use of microtine rodents at eyries on the Seward Peninsula, Alaska, but suggested that microtines were important because they attracted other species (i. e., jaegers, Stercorarius spp.; Short-eared Owl, Asio flammeus) which were taken as prey by Gyrfalcons.

Arctic ground squirrels were the most common prey of Gyrfalcons in the study area after the winter snow had melted. This was similar to the observations of summer prey made by Murie in Mount McKinley National Park (Murie 1946, Cade 1960). Averaging all eyrie collections, arctic ground squirrels were present in the prey remains more than twice as often as all other prey items. Prey remains at the 1976 study site (Table 10) were composed almost exclusively of arctic ground squirrels throughout the time from hatching to fledging. At this eyrie, ptarmigan were absent from the diet between 3 June and early September. The remains from two other eyries indicated that ptarmigan were not commonly selected as prey during late June and July and that during this time arctic ground squirrels were the most common prey items.

Arctic ground squirrels began hibernation during September and October (Carl 1962, Morrison 1964) and at this time the prey of Gyrfalcons abruptly changed to ptarmigan and migrant birds. The return to preying upon ptarmigan occurred at a time when large autumn flocks form and when the molt to white winter plumage made the ptarmigan more visible. Molting ptarmigan were probably more visible to predators during autumn because appreciable snowfall does not begin until early October. Their white coloration would be noticable against the vegetated terrain. Once the landscape was snow-covered the ptarmigan would benefit from their cryptic coloration.

Shifts in prey species selected by Gyrfalcons during the breeding season have been previously reported by Kistchinski (1957), Cade (1960), White (1964), White and Cade (1971) and Beebe (1974). All these authors have described changes in prey use which were related to the lack of availability of ptarmigan. White (1964) and White and Cade (1971) reported shifts from ptarmigan to arctic ground squirrels by Gyrfalcons nesting on the Colville River. The shift in prey use they described was similar to the seasonal shifts that occurred in the Alaska Range, but in the Colville Region the ptarmigan disappeared suddenly during unfavorable weather conditions in the foothills of the Colville drainage. A similar exodus of ptarmigan was not observed in the Alaska Range. Instead, the total population

of ptarmigan had a lower density in the summer hunting range of the falcons because the winter flocks had dispersed.

Gyrfalcons were opportunistic in their selection of available prey. Cade (1960) observed Gyrfalcons preying on avian lemming predators (e. g. Short-eared Owl and jaegers) at a time when shorebirds and waterfowl were locally abundant. Roseneau (1972), emphasizing the secondary effects of high populations of microtine rodents, recorded a similar situation when ptarmigan were locally abundant. Cade (1960) suggested that owls and jaegers were the easiest species to catch among the available prey species.

In this study area, heavy predation on arctic ground squirrels was observed when waterfowl were locally abundant. The ground squirrels were probably selected as principal prey because they were easier to catch than the waterfowl that were present (e. g., Pintail, Anas acuta; Green-winged Teal, Anas crecca; American Wigeon, Anas americana; scaup, Aythya sp.; Oldsquaw, Clangula hyemalis). Bengtson (1971) recorded increased summer predation by Gyrfalcons on waterfowl when ptarmigan (the preferred prey) were locally depressed. It is probable that waterfowl would have been used as prey in the study area if the local populations of arctic ground squirrels had been lower.

In Gyrfalcons, the functional response to abundant prey (Holling 1965) varies depending on location and individual birds. Roseneau (1972) provided detailed information on the

variations in prey taken by Gyrfalcons nesting in interior and coastal regions. In many cases not all of the potential prey species near the nest site were captured as prey. Some pairs relied heavily on a diverse group of migrant birds and some pairs were monotonously steadfast to resident species, especially ptarmigan. Hagen (1952) and Cade (1960) described the Gyrfalcon's 'set' on ptarmigan, indicating that ptarmigan were selected as prey whenever possible.

In areas where arctic ground squirrels occur in Gyrfalcon nesting localities, these mammals are clearly an important summer food. Arctic ground squirrels are present when fledgling Gyrfalcons are developing hunting skills. During this time it is probable that a prey specific search image (SSI; concept defined by Tinbergen 1960, qualified for raptors in Mueller 1974b,c) for arctic ground squirrels becomes entrained in the young falcons. The development of a SSI may increase the predatory success in raptorial birds (Mueller 1975, 1977; Johnson 1978). Since varying responses to abundant prey resources have been reported, it is probable that Gyrfalcons rely on a suite of SSI's to assure predatory success. In interior or inland nesting situations, ptarmigan and arctic ground squirrels are often the most abundant prey available to Gyrfalcons. It would be advantageous for young Gyrfalcons to develop a SSI for these species and other locally abundant species.

Male Hunting Activity

The male Gyrfalcon did most of the hunting throughout the nesting season and therefore contributed a major influence on the spring-summer diet and seasonal use of prey species of a nesting pair. During courtship and thereafter, the male provided the female with food so that until the mid-nestling period the female did not hunt. Even after the female resumed hunting activities, the male continued to deliver prey to her and the nestlings. Because hunting was mostly performed by male falcons, most of my observations have been made of the male Gyrfalcon.

A total of 36 male hunting forays were observed during 1975 and 1976. A departure of the bird from the nest-cliff through to its subsequent return to the area was used to define a single hunting foray. Table 13 lists the forays conducted by the male at the nest studied in 1976. These data (n = 32) were the best record of hunting activity by a single Gyrfalcon during this study. All of these flights occurred after hatching. Hunting forays during the incubation period were not timed.

Of 32 hunting forays timed during 1976, the male returned with prey on 27 occasions. Unsuccessful flights (n = 5) were judged as those that ended when the male returned to the eyrie or nest-cliff without prey. In these instances, the male may have succeeded at capturing prey but ate it before returning to the eyrie. Observations of this

Table 13. Hunting flights by the adult male Gyrfalcon during the nesting season, Alaska Range, 1976.

Date	Age of chicks	Number of flights observed	Flight time in minutes (mean)	Number successful	Number unsuccessful	Prey captured
4 June	1	2	36,282 (159)	0	2	-
8 June	5	1	198	1	-	unknown
10 June	7	3	82,224,128 (145)	1	2	ground squirrel
12 June	9	1	70	0	1	-
13 June	10	1	55	1	-	ground squirrel
25 June	22	2	28,153 (91)	2	-	ground squirrel, small bird
27 June	24	2	11,74 (43)	2	-	ground squirrel
28 June	25	2	162,172 (167)	2	-	ground squirrel
29 June	26	3	30,47,172 (83)	3	-	ground squirrel, unknown
30 June	27	2	53,72 (63)	2	-	ground squirrel, unknown
2 July	29	3	70,125,134 (110)	3	-	American Robin, ground squirrel, unknown
3 July	30	3	8,23,180 (70)	3	-	ground squirrel, unknown
4 July	31	3	13,28,78 (40)	3	-	ground squirrel, unknown
5 July	32	1	19	1	-	ground squirrel
10 July	37	1	45	1	-	ground squirrel
17 July	44	2	35,121 (78)	2	-	ground squirrel
		32	$\bar{x}$ = 99	27	5	

behavior have been recorded previously in Gyrfalcons (Muir 1974), Peregrine Falcons (Nelson 1970) and other raptor species. In this study, when the male returned without prey, his crop was not enlarged (indicating a lack of recent feeding) and it was doubtful that prey were captured during these forays.

The duration and some characteristics of male hunting forays are given in Table 13. The mean length for all forays was 91.2 minutes, less than the mean duration for hunting reported by Platt (1977). These differences may have been caused by differing prey resources or the skills of the individual falcons. No difference was found between the length of time for successful versus unsuccessful forays (t test: $t = 1.90$, $p < 0.05$, $df = 3$). Platt (1977) also found that the length of successful hunting flights of Gyrfalcons did not differ significantly from that of the unsuccessful flights.

The frequency of male forays from the nest-cliff (presumed hunting flight) varied from one to five flights per day. On 3 July, five forays were documented and three of them were timed completely. The longest foray lasted at least 465 minutes (still in progress when observation ended). The shortest flight was a successful foray lasting only eight minutes.

The length of the hunting forays made by the male during the early nestling stage were not significantly different from the length of the flights made by him near the time of fledging, although the data suggest a trend of decreasing time per foray (Figure 8). This could be explained by a need for the male to provide more food to the nestlings as they increased in age. The shorter forays correlated with the emergence of young arctic ground squirrels. The increased availability of vulnerable prey probably reduced the time required for hunting. The emergence of young arctic ground squirrels occurred while the young falcons needed large amounts of food for growth and development. The correlation between high nestling food demands and increased availability of ground squirrels may result from an evolutionary adaptation in the reproductive biology of Gyrfalcons.

Juvenile arctic ground squirrels were an important prey resource for fledgling Gyrfalcons that were learning hunting techniques. Young ground squirrels were driven from adult territories during the time of fledging and their naive movements made them vulnerable to predation, even by inexperienced falcons. A similar relationship existed between the fledging of Gyrfalcons and the hatching of young ptarmigan (Cade 1960). In this case, fledgling Gyrfalcons have the opportunity to learn to hunt as the ptarmigan chicks are learning to fly. Thus, the reproductive cycle of

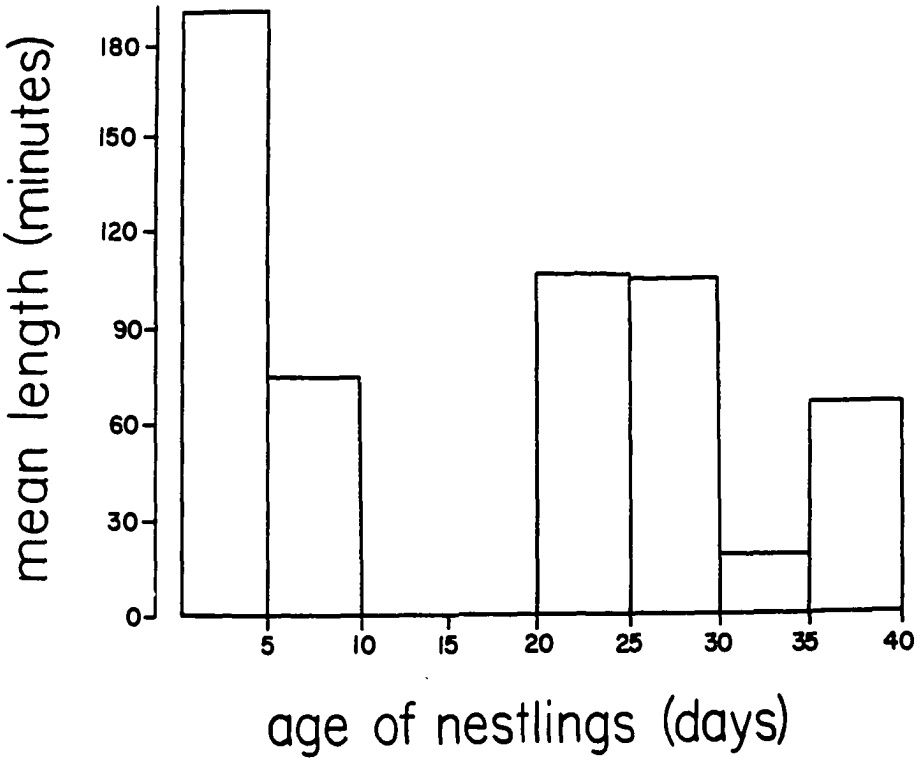

Figure 8. Length of adult male hunting forays during the nestling period of Gyrfalcons in the Alaska Range, 1976.

Gyrfalcons is timed to maximize the use of resident prey species (ptarmigan and ground squirrels).

The hunting range of the male Gyrfalcon was located away from the nest-cliff. The assessment of remote hunting ranges was based on direct observations of male birds that disappeared from binocular-aided sight before they exhibited any flight characteristics suggestive of actual hunting activity (Rudebeck 1950-51, White and Weeden 1966, Bengtson 1971). Platt (1977) described similar departures by the male that resulted in the bird disappearing in a clear sky when viewed with 8 power binoculars. Cade (1960) and White and Cade (1971) have also observed Gyrfalcons returning with prey that were probably captured more than 10 km from the eyrie. Muir (1974) observed Gyrfalcons that returned with prey (juvenile tundra hares), at a time when surveys of the nest site locale revealed a lack of similar age-class hares.

The male Gyrfalcon used two methods of flight when he left the nest-cliff to begin hunting forays. One type was direct level flight characterized by steady wing beats, moderate elevation (10 - 30 m) and little deviation in course of flight. The second type of departure relied upon soaring flight; the male circled above the nest-cliff to a high altitude (>100 m) and then moved slowly away. Direct level flight was used when flying toward relatively flat landscapes or lowlands scattered with willow thickets, lakes and ponds. Soaring departures coincided with hunting over

rocky uplands that had moderate topographic relief. Orographic air currents or thermal drafts may have induced and aided the soaring flight that was associated with hunting over hilly landscape.

The maximum distance that the male traveled during daily hunting flights is not known. However, some information on the distances the male hunted from the nest site was collected during incubation. The male was sighted 9.6 km from the nest while returning with prey. Appearing labored in flight, the male stopped to rest on a small knoll. Since the adult was fatigued, it was possible that the prey was captured at much greater distances (15 - 20 km) from the nest. On another occasion several weeks after hatching, the male was perched on a gravel ridge 8 km from the eyrie. The bird may have been hunting from the perch. Another gravel slope overlooking a broad valley was used frequently by Gyrfalcons during the nestling season (Jack Johnson, personal communication, 1976). This area was located 6.5 and 12.0 km from the nearest eyries. Although not confirmed, it was likely that the bird observed in this circumstance was the hunting male from the study site.

The male was never observed hunting near the nest-cliff. Even when supplemental prey was released near the nest (maximum 0.5 km from the nest), the male showed no interest in hunting close to the nest. Other rocky uplands and gravel ridges within 5 km of the nest provided excellent

habitat for arctic ground squirrels. The abundance of prey near the nest cliff apparently did not attract the male during his hunting forays.

It is not clear why the male traveled such long distances during hunting forays when prey was available close to the eyrie, although size dimorphism may have contributed to differing uses of prey resources (White and Cade 1971, Snyder and Wiley 1976). A strategy of partitioning prey resources also may have evolved between the male and female of a pair whereby the male hunts at more distant locations. The male may have avoided hunting in localities near the nest to minimize predation pressure so that the female and fledglings may be more successful when they begin hunting later in the summer.

Female Hunting Activity

Female Gyrfalcons did not hunt for prey during late courtship, incubation and the early nestling phase. Hunting activity was initiated when brooding of the young ceased. The transition from brooding to active hunting was gradual. Typically, the female interrupted brooding periods by perching near the nest. Early perching activities included preening and dozing, but later, activities such as head bobbing and flight intention movements were common. The female made regular flights from perches on the nest-cliff when the young were 23 days old.

A total of 22 female hunting flights were observed during 1976 (Table 14). The first flight, from a nest-cliff perch, occurred when the young were 17 days old and 13 days before the last brooding of the chicks by the female. The last hunting flight was observed just prior to fledging of the young falcons.

The length of female hunting forays varied with the prey taken and the time elapsed from the resumption of hunting (Figure 9). For example, chickens released within sight of perches used by the female were either captured quickly or left unhunted for long periods or time. The first chicken was taken as prey 96 minutes after the female left a perch on the nest-cliff. Much of the time may have been spent locating the release stations or ascertaining the 'quality' of the prey at the stations. The short hunting time (3 minutes) required for the next chicken kill indicated that the female may have simply revisited the location where she had been previously successful.

The time required to capture arctic ground squirrels varied from 2 to 55 minutes. Successful flights that resulted in captures of ground squirrels were not significantly shorter than flights that ended with the capture of chickens (t test: $t = 1.97$, $p < 0.05$, $df = 12$).

Some successful hunting flights by the female Gyrfalcon were remarkably short (Table 14). Several flights lasted less than five minutes and occurred when the female departed

Table 14. Hunting flights by the adult female
nesting season, Alaska Range, 1976.

Date	Age of chicks	Number of flights observed	Flight time in minutes (mean)
20 June	17	1	96
21 June	18	1	3
22 June	19	6	2,4,2,5, 2,7 (4)
26 June	23	1	16
28 June	25	1	32
30 June	27	1	3
2 July	29	3	12,53,48 (38)
3 July	30	3	11,40,106 (52)
6 July	33	2	2,20 (11)
9 July	36	1	5
13 July	40	2	3,25 (14)
		22	$\bar{x}$ = 23

Gyrfalcon during the

Number successful	Number unsuccessful	Prey captured
1	-	chicken
1	-	chicken
1	5	ground squirrel
1	-	ground squirrel
1	-	ground squirrel
1	-	ground squirrel
2	1	ground squirrel, chicken
3	-	ground squirrel, chicken
1	1	ground squirrel
1	-	ground squirrel
2	-	ground squirrel
15	7	

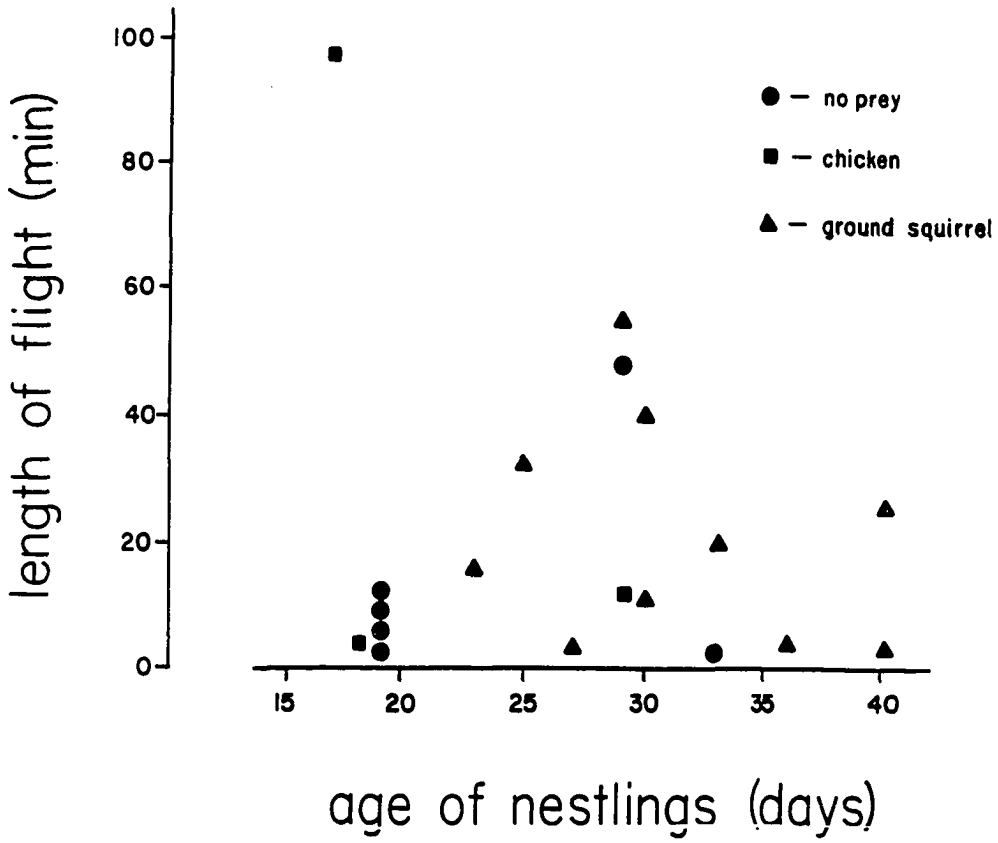

Figure 9.. Length of adult female hunting forays during the nestling period of Gyrfalcons in the Alaska Range, 1976.

the nest-cliff and returned with freshly captured prey. Invariably these flights were preceded by head bobbing intention movements, indicating that prey was sighted from the nest-cliff perch. However, the actual taking of prey was not observed in these instances and the possibility exists that the short hunting flights may actually have represented distant prey transfers from the male Gyrfalcon returning with prey. Nelson (personal communication, 1979) observed prey transfers between male and female Gyrfalcons at more than 1.5 km from the nest site of the pair. The lack of wailing vocalizations by the female (as she departed) suggested that these observations were not remote food transfers but instead represented actual hunting flights.

Direct observations and locations determined by radio telemetry triangulation indicated that the female Gyrfalcon hunted close to the nest-cliff while the young were in the nest. While tagged with a radio transmitter, the female did not move more than 3 km from the nest site. These observations were made when the young falcons were 9 to 17 days old. As fledging approached, the female spent less time near the eyrie. These absences suggested that the female was hunting at greater distances from the eyrie.

Response to Supplemental Prey

Supplemental prey was released to examine predation in nesting Gyrfalcons. During 1975, 19 chickens were released during the nestling period and 15 were taken as prey. In 1976, 40 chickens were released and 25 were taken as prey by Gyrfalcons. Table 15 presents information on the fate of released prey.

Only the female Gyrfalcon was observed taking prey. Several predatory characteristics were noted when this occurred. The male never showed an interest in the supplemental food and he did not attempt to capture the chickens. Chickens that died before being found by the falcons were never taken or removed from the release sites. In these cases, the dead chickens were left at the release stations for 24 - 48 hours, but they were accompanied by live chickens. Prey was usually killed within 24 hours of release. Even though chickens were presented steadily in 1976, other natural prey were taken by the female. Some chickens were not taken as prey even though other members of the same release group were taken. Chickens were able to escape predation by hiding in dense thickets of willow (Salix spp.) and dwarf birch (Betula glandulosa).

The capture of supplemental prey showed that Gyrfalcons quickly recognize a vulnerable prey resource. In 1976, the decreased time required for prey capture between 11 June and 2 July probably reflected a conditioned response to the prey

Table 15. The fate of chickens, Gallus gallus, released as supplemental prey near Cyrfalcon nesting sites in the Alaska Range.

Release date	Number released	Time elapsed for first capture (hrs)	Time elapsed for last capture (hrs)	Use of prey
Eyrie No.1				
5 June 1975	1	3.5	-	Fed at nest.
5 June 1975	1	3	-	Fed at nest.
5 June 1975	2	-	-	Not taken.
6 June 1975	4	?	48	1 died (not taken), 3 taken.
6 June 1975	1	20	-	Fed at nest.
6 June 1975	1	-	-	Died and not taken.
6 JUne 1975	1	20.3	-	Uncertain.
8 June 1975	3	-	22.4	2 fed at nest, 1 not taken.
9 June 1975	3	2.7	?	2 fed at nest, 1 not taken, 1 died and not taken.
Eyrie No.2				
11 June 1976	6	24	168	All fed at nest, 1 cached after feeding.
18 June 1976	6	?	<24	4 fed at nest, 3 cached after feeding.
20 June 1976	3	8	12	2 fed at nest, 1 cached after feeding; 1 uncertain use.
27 June 1976	5	<22	72	4 fed at nest, 1 not taken.
2 July 1976	2	0.4	1	2 fed at nest, 1 cached after feeding.
5 July 1976	2	-	-	2 not taken.
8 JUly 1976	2	?	<48	Uncertain use.
16 July 1976	2	?	<18.5	2 partly eaten and left on tundra.

available at release stations. Even so, the amount of supplemental prey that was used may simply be influenced by the catch of natural prey items (e. g., supplemental prey was taken when natural prey had not been captured). In all cases the Gyrfalcons were free to choose their prey items (either natural or released prey).

The Gyrfalcons exhibited no interest in dead supplemental prey even though some authors have reported the use of carrion among falcons. Stevens (1953) found that Gyrfalcons used carrion when other food sources were scarce. Langvatn (1977) found evidence of reindeer (Rangifer tarandus), marten (Martes martes), and red fox in castings. He suggested that these items were not normal quarry of the Gyrfalcon. Instead the falcons probably found these items as carrion. Muir (1974) constructed a blind near a Gyrfalcon eyrie and fed the adults sections of freshly killed tundra hare. He found that the adults accepted the 'prey' and carried it to the nest to feed the young.

The feedings conducted by Muir (1974) occurred under circumstances similar to the conditions of this study. The major difference was that Muir provided natural prey as carrion. Even though live chickens were taken as prey, it was possible that dead chickens were not recognized as prey. As an alternative explanation, the individual falcons may have possessed different predatory standards such that carrion was accepted in one case and not the other.

Predation Strategy

Ultimately, predation in raptors is governed by evolutionary processes because successful predation enables individuals to survive. The success of individuals ensures the success of the species. Differing conditions of food supply and reproductive success may govern the strategies used by the predator. Among predators in general, Slobodkin (1962,1964) described prudent and imprudent predators. Prudent predators are those that maximize their own food supply while minimizing the possibility of pressuring prey populations into a depressed population level. Imprudent predators take prey in excess of their necessary requirements and as a result may exert considerable pressure on prey populations.

Brosset (1973) examined the ontogeny of predation in Falconidae and other Accipitrine raptors and concluded that active predation was practiced by Accipiters and passive predation was a characteristic of falcons. Hunting was often heightened by some prey species responses (e. g., movement, intent to flee) and Brosset acknowledged that the prey stimulus-response factor was important in eliciting predatory activity in all raptors. Mueller (1974b, 1975) suggested the importance of innate recognition of prey in raptors with some benefit of experience conditioning.

Nelson (1977) stated that Peregrine Falcons harvested prey on a sustained yield basis and practiced 'natural conservation'. Yet, he acknowledged that Gyrfalcons use prey bases that are cyclical (at least in part, e. g., ptarmigan and hares) and therefore possess predatory traits of raptors using unstable prey resources. These characteristics include nomadism, adjustments in territory sizes and modification of clutch sizes. Gyrfalcons also have reproductive characteristics associated with dependence on stable prey resources (e. g., synchronous hatching, defense of hunting range, variation in territory types, Nelson 1977). Use of differing territory types ensures a harvest of the minimum required prey on a sustained yield basis. Nelson concluded that evolutionary fitness of falcons, especially Peregrine Falcons, has been regulated by an equilibrium of 'food supply-territory size-nest site' relationships. Deviations from the equilibium produces decreased fitness because of over harvest of prey resources or wasted energy in defense of an overly large territory.

The observations of changes in seasonal prey selection and positive response to supplemental prey clearly establish that Gyrfalcons were opportunistic predators in the proximal time frame. The falcons took prey as it appeared, killed in excess of needs and cached prey for later use. These responses were understandable considering the vagaries of annual prey abundance, temporal changes in diurnal activity

of prey under periods of changing day-length, variations in prey availability resulting from weather or other extrinsic factors and the increased demand for prey during the period of nestling growth and development.

Opportunistic characteristics also are advantageous in the ultimate or evolutionary sense because the Gyrfalcon breeds in a harsh and sometimes highly variable environment. Opportunistic predation selects for individuals which have optimized predatory efficiency and have been able to survive widely varying circumstances. Northern regions provide less advantage for harvest on a long term sustained yield basis (as described by Nelson 1977), because the occurrance of a wide variation in annual prey abundance is typical. There has been no advantage or reason for Gyrfalcons to practice 'natural conservation' or prudent predation.

The observed use of supplemental prey by Gyrfalcons has suggested several other predatory characteristics of the species. The female demonstrated a capability to recognize locally vulnerable prey species and learned to take new prey species. Successful prey capture gave experience that was used at later times to search for new prey. The Gyrfalcons were responsive to and learned that supplemental prey release sites frequently offered suitable prey. Responses to released prey indicated that prey availablility

influenced predation. Similar relationships between abundance of prey and hunting success of raptors have been witnessed in other areas (Galushin 1974).

SUMMARY

Observations in winter and the early breeding season show that some Gyrfalcon pairs remain at nest-cliffs throughout the winter, whereas other pairs arrive at nest-cliffs during the spring. Regardless of the timing of occupancy, aerial displays were used to advertise the presence of the pair at the nesting-cliff. These flights were characterized by soaring or energetic diving between the pair of birds.

Once established at a nest-cliff, the roles and duties of each sex of the pair were different. Beginning during courtship, the female did not hunt, but received prey from the male. During incubation, the female was sedentary at the nest site and performed most of the incubation. In contrast, the male incubated for short shifts, usually while the female consumed prey that had been received from the male. Both sexes show increased interest in incubation just prior to and during hatching. The movements of incubating birds included a variety of postures and activities as they repositioned themselves above the eggs. 'Wing pumping,' an unusual sequence of wing movements similar to the actions of birds making a nesting scrape, was performed by an incubating female.

During the nestling period, brooding and feeding of the young were the major activities of the female Gyrfalcon.

The male did not brood often, but continued to provide food for his mate and nestlings. Shading of the chicks from direct sun was observed frequently when the young were 20 - 27 days old. Adults and young panted when exposed to these sunny conditions. Feedings of the young were performed by the female Gyrfalcon on most occasions. The male transferred prey to the female for these feedings. Prey transfers were observed at the nest site, perches near the nest, and during flight. During aerial transfers, the female positions herself below the male, makes a half-roll, and uses her feet to catch prey released from the beak of the male. Food-bringing (dropping food at the nest rim) was also used by both adults.

Caching of prey by adult Gyrfalcons occurred regularly if prey was not consumed by the nestlings. All cachings were observed in areas of rock cliff, talus slope or vegetated slope located near the nest site. Cached prey was often retrieved for feeding to nestlings and six recachings of prey were observed.

Identification of prey remains collected at intervals throughout the breeding season showed evidence of seasonal variations in prey use. The Gyrfalcons relied on ptarmigan until arctic ground squirrels emerged from hibernation. Thereafter ground squirrels represented most of the summer food. When ground squirrels began hibernating in the fall, ptarmigan were the common prey species. The male Gyrfalcon

secured most of the prey during the entire breeding season and his role in hunting cannot be overemphasized. Direct observation of the male during hunting foray departures indicated that the hunting ranges used by the male were located away from the nest-cliff. The male returned with prey on most (84 %) of the observed hunting forays and as many as five flights were observed in one day.

The female did not hunt until brooding of the young decreased. The transition from brooding to active hunting was gradual and began when the young were less than three weeks old. Locations based on radio telemetry triangulations and direct observations showed that the female did not move more than short distances from the nest during the early nestling stage. Near fledging, the female was absent for much longer periods of time and she may have been hunting at greater distances from the eyrie.

Responses to supplemental prey released near nest sites showed that the falcons recognized vulnerable prey and quickly learned to take new prey species. However, the adults differed in their response. All supplemental prey was taken by the female, usually within 24 hours of release. The use of released prey increased through time, suggesting that the female learned to search for the prey released at the feeding stations. These prey releases were conducted outside the hunting range normally used by the male and within the range used by the female.

These experimental studies indicated that Gyrfalcons may be classed as opportunistic predators. They responded directly to differing availabilities of prey and excess prey were killed and cached for later use. This strategy of predation is adaptive in arctic environments because annual variations in prey abundance are common. Harvesting maximum sustained yields of prey, as practiced by falcons in more temperate areas, would be less advantageous because the prey source in northern regions is not stable.

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